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Baited underwater camera studies of the biodiversity and abundance of animals in the temperate, tropical and Antarctic marine environment

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Submitted in fulfillment of the requirements for the Degree of Doctor of Philosophy

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Abstract

Baited underwater camera (BUC) systems are becoming popular in the shallow water environment to monitor the relative diversity and abundance of fish and invertebrate assemblages. This thesis describes methods developed to use BUCs in temperate, tropical and Antarctic environments and their application to questions concerning the factors controlling shallow water marine biodiversity and abundance. In Chapter 2 the design and development of a BUC system suitable for attracting, identifying and counting temperate shallow water (< 30 m) fish and crustacean species on the West coast of Scotland is described. The use of BUC systems has been limited in temperate waters and a cost- and – time efficient method could be valuable to monitor the before and after impact of the proposed Scottish Marine Protected Area network. As a test of the BUC, deployments were made in Lamlash Bay no-take zone (NTZ) and in two control open sites to provide baseline data early in the life of the NTZ against which future BUC studies can be compared. The tropical Gulf of Aqaba supports unique coral reef fish assemblages and it is important to perform a study specific in this distinct biogeographical region to understand whether BUC surveys could be useful in this sensitive environment. In Chapter 3 we therefore compared the predatory fish assemblages recorded in BUC deployments to the established method of Underwater Visual Census (UVC) surveys in the northern Gulf of Aqaba. Abundance metrics from the arrival pattern of fish at the BUC did not correlate with population abundance estimates from UVCs and it was concluded that until improved methods of interpreting BUC data are developed the deployment of BUCs could be used to assess predator species richness but is not able to indicate relative variation in population abundance. Chapter 4 demonstrates how BUC systems can be used to gather data on a complicated ecological question in extreme conditions. A BUC system was used to examine the distribution of scavenging fauna in relation to the spatial variation in exposure to iceberg impacts experienced at difference iceberg scouring conditions and depths within Marguerite Bay. The results indicate that different scavenger species are adapted to high and low iceberg scouring environments and that they are distributed in accordance with the recognised pattern of decreasing iceberg scouring frequency with depth. The above studies used relative measures of abundance such as recording the highest number of individuals observed at a single time (Max_N). Such measures are limited in their usefulness but there are no robust means of estimating absolute abundance, especially for complex shallow water systems. In Chapter 5 a modelling approach, using a stochastic

simulation, was developed and used to estimate population abundance for species commonly observed in the above studies. Model abundance estimates were generally found to be comparable to those from corresponding UVC transects. This modelling approach has the potential to substantially improve the ability of BUC systems around the world to assess fish and invertebrate diversity and abundance.

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Authors Declaration

I declare that, except where explicit reference is made to the contribution of others, that this dissertation is the result of my own work and has not been submitted for any other degree at the University of Glasgow or any other institution.

Signature _____

Printed name _____

Abbreviations

BUC	Baited underwater camera
UVC	Underwater visual census
MPA	Marine Protected Area
Max _N	Maximum number of individuals observed at the BUC at once
t _{arrival}	Time to the arrival of the first individual at the BUC
t _{maxN}	Time to reach Max _N

1. Chapter 1. Overview

1.1. What is Marine Biodiversity?

Marine biodiversity is the biological variation of the organisms of the marine environment and most commonly describes the number of species in an area (Clarke and Johnston 2003, Costello and Wilson 2011). Marine biodiversity also describes genetic and ecosystem diversity; the genetic variation of individuals within and between species (Gray 1997, Mace et al. 2012) and the diversity of habitats and biological processes that species inhabit within a specific region (May 1994, Bianchi and Morri 2000, Purvis and Hector 2000, Laikre et al. 2010, Ellis et al. 2011, Mace et al. 2012).

To date around 200,000 – 300,000 marine species have been described, not including microbial diversity. This makes up less than one fifth of the world's described species (Gray 1997, Clarke and Johnston 2003, Sala and Knowlton 2006), even though the marine environment represents 90 – 99% of the Earth's habitable space (Vega and Wiens 2012). Terrestrial species diversity is elevated by 400,000 beetle species (Gray 1997) and the high diversity of recorded fungi and nematodes (May 1992, Clarke and Johnston 2003). It is hypothesised that recorded species are but a fraction of the species on Earth, particularly in the marine environment (Grassle and Maciolek 1992, May 1994, Carr et al. 2003, Tittensor et al. 2010). Mora et al. (2011) estimated that 86% of species, 99% in the marine environment, remain to be discovered. Marine life began in the benthic sediments and still the majority of marine species are found there (Angel 1993, Gray 1997). The deep-sea benthic habitat covers 65% of the earth surface (Danovaro et al. 2008) and has been identified as potentially supporting between 10 million (Grassle and Maciolek 1992) and 500,000 (May 1992, 1994) undiscovered species.

Even though marine species diversity is low compared to the terrestrial environment (Bianchi and Morri 2000) it represents all of the Earth's 35 animal phyla, and 14 endemic phyla, while the terrestrial environment supports only 11 and the freshwater 14, none of which are endemic (Ormond 1996, Gray 1997, Snelgrove 1999, Bianchi and Morri 2000, Carr et al. 2003).

1.2. Why is Marine Biodiversity Important?

The management of human activities inside the marine environment often focuses on the preservation of ecosystems and the services they provide to humans (Bulling et al. 2010, Mace et al. 2012). Ecosystem services are “the benefits provided by ecosystems that contribute to making human life both possible and worth living” (as defined by the UK National Ecosystem Assessment). Some ecosystem services involve the provision of products or materials, such as food from fisheries, flood defences and waste removal (Worm et al. 2006, Palumbi et al. 2009, Barbier 2012). Non-material ecosystem services include the recreation and spiritual benefits provided by the natural environment (Harmon and Putney 2003). Biodiversity also has an intrinsic value that refers to the value of the entity itself, independent of its potential usefulness to human beings (Rolston 1986, Callicott 1989). Those supporting the intrinsic value of biodiversity believe that it and the moral issues regarding stewardship of the marine environment are important to consider when developing conservation measures (Ghilarov 2000, Warwick and Clarke 2000, Dayton et al. 1995).

Providing evidence of the links between biodiversity and ecosystem services is believed to be important by many ecologists to demonstrate the importance of preserving marine biodiversity (Ghilarov 2000). Examination of the link between terrestrial biodiversity and the provision of ecosystem services has primarily involved the experimental manipulation of species diversity and an examination of the impact on the ecosystem processes that produce services (Tilman 1996, Schwartz et al. 2000, Balvanera et al. 2006). A meta-analysis of data from 103 publications examining biodiversity-ecosystem functioning clearly indicated that biodiversity has a positive link with ecosystem services (Balvanera et al. 2006). Two primary mechanisms have been identified as increasing ecosystem functioning with increased species diversity. The first mechanism describes that high species diversity increases the chance of the presence of species key to the production of ecosystem services. Secondly, that more species increase the chance of facilitation, where one species improves the environmental conditions for another, and complementary resource use. Complementary resource use occurs if more species are present to use resources at different points in time and space allowing the full range of resources to be used more efficiently thus increasing the productivity of the system and reducing the loss of resources (Hooper et al. 2005, Palumbi et al. 2009). These processes are common within the marine environment (Palumbi et al. 2009). However, a review by

Schwartz et al. (2000) concluded that few studies provide an empirical link between biodiversity and ecosystem functioning and that the impact of diversity is more complex (Duarte 2000) and requires further scientific attention to distinguish the impact of biotic and abiotic factors and community structure (Schwartz et al. 2000, Hooper et al. 2005).

Recently more scientific attention has been made to uncover the links between biodiversity and ecosystem function in the marine environment (Raffaelli and Friedlander 2012). For example, one study of global seagrass communities found an overall positive link between increasing species richness and ecosystem services. Assemblages with high species richness are generally more likely to be characterised by a mixed-species assemblages with a wide range of forms. This increases their functional diversity, which will enhance complementary resource use and the ability to remain productive in the resource limiting environment that seagrass often inhabits (Duarte 2000). A meta-analysis of trends in regional biodiversity and services from coastal ecosystems found that ecosystems with naturally high regional species richness had a lower rate of collapse and loss of commercially important fish and invertebrate species. Systems with low biodiversity, from previous human impacts, experienced more losses in the functioning of ecosystem services including the support of viable commercial fish populations and nursery habitats and water filtering and detoxification effects (Worm et al. 2006). A study of deep sea benthic biodiversity in relation to measures of ecosystem function across a range of global habitats found a positive exponential relationship (Danovaro et al. 2008). Benthic biodiversity is an effective measure to examine the relationship between biodiversity and ecosystem function because of its importance in global carbon and geochemical cycling (Snelgrove, 1999).

Marine biodiversity and ecosystem services are under increasing pressure as human populations expand (Worm et al. 2006, Ellis et al. 2011, Sadovy de Mitcheson et al. 2012) and rates of habitat loss, fishery overexploitation, pollution, climate change and oceanic biochemical changes also increase (Dulvy et al. 2003, Sala and Knowlton 2006, Worm et al. 2006). Rich biodiversity allows species and communities to maintain their functionality in the face of human pressures because it provides a wider range of possible adaptations to ensure survival (Bianchi and Morri 2000, Ehlers et al. 2008, Chiarucci et al. 2011) as has been supported by both experimental and theoretical studies. For example, the sockeye salmon in Bristol Bay, Alaska, has a high diversity of life history traits, or phenotypic diversity. This has allowed the productivity of populations to be

maintained under major climatic changes through variation in the timing of spawning , egg sizes and incubation strategies allowing different populations to perform well under a range of environmental conditions (Hilborn et al. 2003). Yachi and Loreau, (1999) used a stochastic model to demonstrate that high species richness reduced the variance and enhanced the productivity of ecosystem processes (Yachi and Loreau 1999).

1.3. Measuring Marine Biodiversity

In order that spatial and temporal patterns in biodiversity can be assessed there is a need for indices which describe quantifiable and relevant aspects of community species richness and the relative abundance (Magurran 2004, Magurran et al. 2010). Even though marine biodiversity encompasses the genetic, species and ecological diversity of marine communities the most common measurement of biodiversity is species diversity, the number of species within a given area (Gray 1997). Several concepts of species definition exist, however, most agree that a species is a genetically distinct group of individuals incapable of producing fertile offspring (Frankham et al. 2012). Species diversity is commonly used as a measure of biodiversity (Bianchi and Morri 2000, Magurran 2004, Chiarucci et al. 2011) as it is easily quantified and understood (Purvis and Hector 2000) but also reflects genetic and ecosystem diversity (Chiarucci et al. 2011). Measures must also be able to encompass the variation in the abundance of individual species within an assemblage (Magurran 2004). Evenness is used as a measure of the similarity of species abundances in an assemblage. An assemblage where each species has equal abundance will have high evenness while that containing a dominant species or species' will have low evenness (Warwick and Clarke 2001, Magurran et al. 2010). It was first suggested by Vane-Wright et al (1991) that measures should also consider the taxonomic relatedness between species, particularly for the purposes of conservation. A measure of community taxonomic distinctness was developed which is based upon the distinctiveness of a species compared to the rest of the community (Ricotta 2004). One drawback of this measure is that detailed information on the relatedness of most groups, such as resolved cladograms, is often unavailable and the only information on relatedness is from basic Linnean taxonomy based on morphological or functional differences (Ricotta, 2004). Measures of diversity are susceptible to changes in sampling effort (Magurran 1988) and it is therefore important to measure the sampling effort used to produce indices (Soetaert and Heip

1990). This can be a problem when sampling over large spatial areas and long time scales, common when monitoring the marine environment (Warwick and Clarke 2001). Over spatial scales species diversity can be partitioned into alpha, beta and gamma diversity, initially by Whittaker (1960). Alpha diversity describes species diversity within an assemblage inhabiting a specific ecological area or habitat (Whittaker 1972, Duelli and Obrist 2003). Beta diversity refers to how the local species diversity, described by alpha diversity, varies between assemblages across spatial and temporal gradients (Noss 1983, Harborne et al. 2006). Gamma diversity encompasses the overall species diversity of the ecosystem within which alpha and beta diversity exist (Whittaker 1972, Arellano and Halfpeter 2003).

1.4. Spatial Patterns in Marine Biodiversity

Marine biodiversity varies across the temperate, tropical and polar regions (Petersen and Curtis 1980, Sala and Knowlton 2006). For many taxa and guilds both shallow and deep water marine species diversity declines from the tropics to the polar regions (Sala and Knowlton 2006, O'Loughlin et al. 2011), as in terrestrial environments (Rosenzweig 1995, Witman et al. 2004). For example; for corals and fishes (Hughes et al. 2002, Roberts et al. 2005), molluscs (Roy et al. 1996, Witman et al. 2004) and bryozoans (Clarke and Lidgard 2000) diversity is highest at the tropics (Petersen and Curtis 1980). Three types of hypothesis attempt to explain latitudinal gradients in the marine and terrestrial environments. These focus upon the ecological and evolutionary processes that create and maintain diversity and the time and area available for processes to operate (Roy et al. 1998, Mittelbach et al. 2007). However, many terrestrial theories are unsuitable as the marine environment has existed over longer ecological and evolutionary time scales and has less dispersal barriers (Gee and Warwick 1996). A widely accepted theory is that the greater energy available from solar radiation in low latitudes supports greater productivity, biomass (Gaston 2000) and metabolic and speciation rates (Kerswell 2006). This explains the latitudinal variation in several marine groups, including marine prosobranch gastropods (Roy et al. 1998) and other marine molluscs (Rex et al. 2005). Central to the evolutionary hypothesis is that the tropical regions are evolutionarily older, allowing more time for diversification and that higher speciation and lower extinction rates are experienced in the tropics (Mittelbach et al. 2007). However, the pattern is different for specific trophic guilds; pelagic (Tittensor et al. 2010) and macro-algal (Silva 1992) species diversity is highest in the mid-latitudes and

benthic diversity is richest in the Antarctic region (Chown 2012). An increase in diversity exists in Antarctica compared to the tropics due to the high diversity of shallow water benthic fauna in Antarctica (Gray 1997, Clarke and Johnston 2003). High rates of speciation in groups able to withstand the Antarctic conditions, such as echinoderms, have been hypothesised to be the result of subsequent isolation and reconnection from ice sheets and release from predation (Clarke et al. 2005, O'Loughlin et al. 2011). It has been generally accepted that the Arctic marine environment is less species rich than the Antarctic continental shelf and supports less endemic species due to similarities with North Atlantic marine fauna (Clarke and Crame, 2010, Dayton et al. 1994).

Patterns of marine biodiversity are complex and debate still exists over which processes have the most significant effect on creating global pattern of marine biodiversity particularly due to a lack of data for many marine groups (Gee and Warwick 1996, Mittelbach et al. 2007). Advances in molecular, phylogenetic and palaeontology techniques and new data from field studies will allow these processes and patterns to be understood further (Mittelbach et al. 2007).

1.5. Threats to Marine Biodiversity

Despite its apparent value, biodiversity losses have been reported in many ecosystems (Worm et al. 2006, Danovaro et al. 2008, Butchart et al. 2010). Declines have been recorded in corals (Carpenter et al. 2008), oceanic predators (Worm et al. 2005), fish (Hutchings and Baum 2005, Worm et al. 2006) but the exact scale of global and local losses can be difficult to quantify in the marine environment due to limited data (Dulvy et al. 2003, Sala and Knowlton 2006). Marine biodiversity declines begin with reductions in the abundance of individual species from population reductions to regional and global species extinctions. The reduction or removal of a species in the marine environment can also cause community wide changes, which can lead to further reductions in the abundance of individual species (Sala and Knowlton, 2006). Data on the changes in marine biodiversity in response to human activities is used to inform management strategies and to allow appropriate actions to be implemented to reduce and counteract losses (Buckland et al. 2005, Ellis et al. 2011).

The extinction rate of marine species is poorly documented, compared to in the terrestrial environment (McClenachan et al. 2012, Snelgrove 1999) however, marine biodiversity is

facing a number of threats that could potentially be causing undocumented species extinctions (Snelgrove 1999). Primary threats include overfishing, pollution, climate change and biological invasions. The combination and interaction of these effects has resulted in the increased loss of marine biodiversity and reduced the resilience of many marine communities to withstand and recover from such threats (Sala and Knowlton, 2006).

1.5.1. Fisheries

Fish represent a diverse marine animal group, particularly due to the high diversity of tropical reef fish (MacNeil et al. 2008, Tittensor et al. 2010), and are integral to the functioning of many marine ecosystems (Pauly et al. 1998). The response of fish biodiversity to fishing activities, resource removal, habitat degradation, pollution and climate change (Cheung et al. 2009, Tittensor et al. 2010, Messmer et al. 2011) must be carefully monitored. Only a small number of fish species, generally predators at the top of the food web, are commercially exploited and their decline in response to fishing has been well documented (Steneck 2012, Jennings 1995). However, these species often have an important functional role in the rest of the fish community and a large body of literature discusses the detrimental effect that their removal can have upon the wider marine community (Coleman and Williams, 2002). The removal of predatory fish by fishing has been proposed to cause a trophic cascade in some marine ecosystems. A fishery-induced trophic cascade is described by Salomon et al. (2010) as “the indirect effects of exploiting marine predators on the abundance, biomass, or productivity of species, or species assemblages, two or more trophic links below the exploited predator”. It has been difficult to detect the effect of a trophic cascade due to the presence of other factors, such as oceanic temperature, that influence fluctuations in prey species (Steneck 1998, Mumby et al. 2012). However, a number of studies claim to have detected fishery induced trophic cascades. The removal of cod from Canada’s Scotian Shelf by fishing has been determined to have caused a fishery-induced trophic cascade by allowing the small pelagic fish species, such as herring, that cod prey upon to increase. Their increase in turn reduced the zooplankton populations the herring feed upon and thus allowed an increase in phytoplankton (Frank et al. 2005). Mumby et al. 2012, provided evidence of changes in the coral reef fish communities in Belize following the removal of groupers through a trophic cascade affecting mesopredators (small-bodied groupers) and damselfish (Pomacentridae). The presence of a fishery-induced trophic cascade was demonstrated in an apex predator addition experiment. More Atlantic cod (*Gadus*

morhua) were re-introduced into a semi-isolated region in the Baltic sea where cod number had declined significantly. Changes in the abundance of species key to the pelagic ecosystem, such as herring, zooplankton and phytoplankton, were monitored before and after the experiment. The addition of the cod caused a decrease in its prey, herring, which allowed zooplankton abundance to increase. This was followed by a decrease in phytoplankton and an improvement in water quality (Casini et al. 2012, Steneck et al. 2012).

Fishing activities using heavy trawl and dredging gear often cause significant physical damage to benthic communities and habitats (Snelgrove 1999, Turner et al. 1999, Thrush et al. 2001). Many fishing activities also catch non-target species (Snelgrove 1999) which become bycatch, “the incidental take of undesirable size or age classes of the target species (e.g. juveniles or large females), or to the incidental take of other non-target species” (Lewison et al. 2004, Hall et al. 2000). Bycatch species can include marine mammals (Bjørge et al. 2002), turtles (Peckham et al. 2007), invertebrates (Bergmann et al. 2001) and fish (Davis 2002). Bycatch species returned to the sea are known as ‘discards’ and their mortality can be increased by injury from capture and release, exposure to light, air and elevated temperatures as well as anoxia (Davis 2002). Even though technical measures have been introduced to reduce bycatch it still represents a serious environmental impact from fisheries (Dayton et al. 1995).

As a result of these impacts fisheries represent one of the greatest causes of declines in the abundance of marine fish (Pauly and Watson 2003, Worm et al. 2006). The biomass of marine fish caught in most areas is either stable or declining (Fernandes and Cook 2013); since the 1950s the removal of fish biomass on a global scale by fishing has increased (Worm et al. 2009) and peaked in the 1980s (Pauly et al. 1998, Clausen and York 2008). The response of fish populations to exploitation is monitored via stock assessments (Worm et al. 2009). Stock assessments of population status quantify aspects of target fish abundance, size and age structure (Worm et al. 2009) and produce estimates of the number of individuals that can be removed and replaced by recruitment to maintain the stock at its maximum growth rate. This estimate is known as maximum sustainable yield (MSY) (Punt and Smith 2001, Hilborn 2010). The stock biomass produced under the MSY, known as the B_{MSY} , is lower than the un-fished biomass (B_0). Recently there has been debate over the state of global fish stocks and their ability to recover (Hilborn 2010, Murawski 2010). Many fisheries scientists believe that the

majority of global stocks are overexploited and this will increase if current fishing levels are maintained (Myers and Worm 2003, Jennings and Blanchard 2004). Single stock assessments and MSY estimates suggest that 63% of 166 stocks analysed had a spawning stock biomass that required rebuilding to reach MSY yet only 28% of the total stocks analysed were experiencing exploitation rates that would achieve this (Worm et al. 2009, Hilborn 2010). An alternative meta-analysis of the links between spawning and recruitment for stocks with various life histories concluded that sustainable fisheries can exist below B_{MSY} and recommended that stocks are maintained at 30 – 40% of unfished stock size (Hilborn 2010).

Consensus has been reached that stocks and exploitation rates differ significantly between fisheries and generalisations mask changes in individual fisheries (Worm et al. 2009, Murawski 2010). For example, when biomass estimates for 144 stocks since 1977 were combined, the decline in North Atlantic demersal (bottom feeding) stocks was masked by increasing North Pacific stocks (Worm et al. 2009). Global marine fisheries are simultaneously stable, declining, collapsing or recovering and assessments and management strategies that focus on individual species or groups are required to achieve recovery (Worm et al. 2009).

Current conclusions on fisheries population trends are primarily based upon stock assessments from the 0.5 million industrial fishers in developed nations while data is limited for 12 million smaller scale fishers, mainly in developing nations (Pauly 2006). Additional data collected on these populations would enable more accurate stock assessments to be made to allow more effective management practices to be designed and implemented (Akpalu and Bitew 2011, Chiarucci et al. 2011). Baseline and long term data sets, that span the life time of the principal organisms and influential environmental factors, are essential to allow changes in the parameters of marine biodiversity to be recognised (Bianchi and Morri 2000, Legg and Nagy 2006, Magurran et al. 2010). Well designed and implemented research and monitoring programmes must be at the core of stock assessments (Pauly et al. 1998).

Stock management by the regulation of fishing effort has achieved various levels of success (Murawski 2010). Successful management programmes all involve clear objectives, the support of the industry and the public as well as precise and regular scientific monitoring programmes (Murawski 2010, Mora et al. 2011). Some

management programmes have been successful in the recovery of depleted fish stocks (Murawski 2010, Eero et al. 2012). For example, controls have reduced the fishing mortality of the Eastern Baltic cod and allowed stock biomass to recover quickly from low levels (Hammer et al. 2010, Eero et al. 2012). North Sea herring spawning stock biomass declined during the 1960s and 70s but has also recovered following the implementation of management strategies (Dickey-Collas et al. 2010).

1.6. Survey and Monitoring of Marine Biodiversity

1.6.1. Fishery - Dependent Data

Monitoring programmes provide data on the diversity and abundance of fish populations which can be used for stock analysis techniques. Virtual population analysis (VPA) is a commonly used stock analysis technique (de Mutsert et al. 2008, Pennino et al. 2011, Heath and Speirs 2012). Virtual population analysis models reconstruct the dynamics of cohorts (fish of the same age and size from a single species and reproductive unit) through time from the analysis of catch data to hindcast the historical abundance of stocks (Ultang 1977, Chen et al. 2008).

However, the reliability of stock assessment based on commercial landings data has come into question (Maunder et al. 2006, Bentley et al. 2012). Landings are affected by catchability, socio-economic values and management, and do not solely reflect the biological changes in the population. It is essential that sampling factors that affect landings are measured and standardised (de Mutsert et al. 2008, Heath and Speirs 2012, Kleisner et al. 2012). Commercial landings are dominated by economically valuable species and sizes in response to market demand as well as the population availability (Heath and Speirs 2012, Sadovy de Mitcheson et al. 2012). It is estimated that 27% of the global catch is discarded because of low commercial value or because sufficient quota is unavailable for landing. Where discards constitute a large proportion of catches, landings data will not accurately reflect fish abundance (Machias et al. 2001). Catches from “Illegal, Unreported and Unregulated” (IUU) fisheries are also not included in landings and even though difficult to estimate, annual levels are thought to be between 11 - 26 million tonnes (Agnew et al. 2009, Borit and Olsen 2012). Between 2006 and 2011 total reported fish landings have been around 90 million tonnes (FAO, 2012). It has been suggested that the focus of stock assessments on biased commercial landings data has

prevented the design and implementation of effective management strategies (Maunder et al. 2006, Apostolaki and Hillary 2009).

1.6.1.1. Fisheries Indicator Species

Indicator species or group are used in fisheries management to assess the effect of fishing on the wider fish communities. For species or groups to be effective indicators their distribution and abundance should reflect changes in fishing impact (Rochet and Trenkel 2002). Marine top predators are effective indicators as they are strongly affected by fishing and are sensitivity to the fluctuations of lower trophic groups (Frank et al. 2005, Sergio et al. 2008, Ruttenberg et al. 2011). Marine predators are functionally important and connections have been drawn between their density and ecosystem productivity and biodiversity levels (Ruttenberg et al. 2011).

A link exists between changes in the size composition of fish communities and fishing mortality as larger fish are generally targeted (Rice and Gislason 1996) and size based metrics are used as effective indicators of the impact of fishing mortality (Greenstreet et al. 2011, Houle et al. 2012). Under the EU Marine Strategy Framework Directive (MSFD) there is a need to develop a more ecosystem based approach to management to conserve marine biodiversity. Fisheries' impacts are considered within the broader conservation objectives for the whole marine ecosystem. (Greenstreet et al. 2008, 2012). This involves the use of 11 descriptors of good environmental status (GES) against which the state of the marine environment is assessed using ecosystem criteria and indicators (Probst et al. 2012). Indicators at the species, habitat and ecosystem level are used (Greenstreet et al. 2012). One of the descriptors of GES deals with the status of exploited fish stocks. Scientific stock assessments are carried out by ICES for a number of commercially exploited fish stocks in European waters however assessments are not available for all exploited stocks (Probst et al. 2012). Indicators have therefore been developed to assess fishery induced changes in the wider fish community. A strong link exists between the abundance of large target fish species and increased fishing mortality and has led to the development of the Large Fish Indicator (LFI), a measure of the proportion of larger fish (> 30 cm) in relation to the total fish biomass, to monitor the dynamics of a number of Northern European fisheries (Greenstreet and Rogers 2006, Fung et al. 2012). Greenstreet and Rogers (2006), analysed 70 years of data from groundfish surveys in the North Sea and found that the LFI was highest in areas of low fishing effort (Greenstreet et al. 2011).

An indicator with a size threshold > 50 cm also reflected changes in small fish biomass in the Celtic Sea (Shephard et al. 2011). The LFI therefore reflects the response of fish communities to fishing impact and has been proposed as a size-and- age based indicator to act as part of an ecosystem indicator of the MSFD (Probst et al. 2012).

1.6.2. Fishery - Independent Data

The use of fishery-independent data dedicated for scientific use removes many of the social and market biases that influence commercially derived data (Fraser et al. 2009, Harms et al. 2010). Independent methods include research trawl surveys, fisheries acoustics (Harper et al. 2010, Rudershausen et al. 2010), egg surveys (Jansen and Gislason 2013), underwater visual census (Brock 1954) and remote sensing (Maina et al. 2008, Ortiz and Tissot 2008).

1.6.2.1. Research Trawls

Trawling is often used as a scientific sampling method to gather information on marine fish populations. For example, in Scottish waters Marine Scotland Science undertakes trawl surveys to gather information on both demersal (fish that live in close association with the seabed) and deepwater fish species which provides abundance at length data (Greenstreet et al. 2012). A long time series of demersal trawl surveys dating back to the 1920s has been collected in many areas. For example, in the Firth of Clyde scientific trawl surveys have been carried out since 1927 (Heath and Speirs 2011). A time series of deepwater trawl surveys (> 500 m) to collect fishery independent data on fish populations along the continental slope of the Rockall Trough began in 1998. The survey have generated indices of fish abundance, size and diversity that are comparable over space and time, as well as the identification and cataloguing of mega-benthos in the area (Neat et al. 2010).

However, established trawl survey methods are not suited in many nearshore areas, owing to shallow depths, obstructions on the sea bed or vulnerable habitats, which has led to a lack of information on fish abundance in these areas (Smith et al. 2010). Some surveys have been carried out in inshore waters by the Scottish Environmental Protection Agency using beam trawls, in combination with Fyke and Seine netting, of estuarine fish communities on the SW Scotland as part of the Water Framework Directive (O'Reilly 2011).

1.6.2.2. *Acoustic Surveys*

Acoustic instrumentation has been used widely by both commercial fishermen and research scientists to detect fish in the marine environment. Acoustic surveys are able to survey a large volume of water quickly and have been important in gathering information on the abundance and distribution of wild fish populations (Gunderson 1993, Simmonds and McLennan 2005). Acoustic surveys are however, not suitable for gathering information on demersal fish or those in close association with the surface where the acoustic signal is disturbed. The method is however widely used for the survey of pelagic species (Simmonds and McLennan 2005). For example in Scotland acoustic surveys are regularly used for the assessment of herring (*Clupeidae*) and mackerel (*Scombridae*) (Walsh et al. 1995) stocks and have supplied data to the North Sea Herring Assessment since 1989 (Simmonds et al. 2009).

1.6.2.3. *Egg Surveys*

The number of eggs in the plankton is proportional to the adult population size and eggs numbers are used to provide measurements of the biomass of some species which can be difficult to sample using trawling (ICES 2012). These species often react to the gear, and other are poorly detected in acoustic surveys due to their lack of a swim bladder. The number of eggs is converted to the number of eggs spawned per m² of seabed per day and used to determine the total annual egg production. The relationship between female weight and egg number is known is used to estimate the total female fish biomass from egg surveys and assuming a sex ratio of 1:1 this information enables an estimate of the entire stock biomass. Eggs surveys have been used to survey the Western stock of Atlantic mackerel (*Scomber scombrus*) every three years since 1977 (Lockwood et al. 1981, Priede and Watson 1993, ICES 2012).

1.6.2.4. *Underwater Visual Census (UVC) Surveys*

Underwater visual census (UVC) surveys by SCUBA divers were initially introduced by Brock (1954) for surveying reef fish populations in Hawaii and have become a common method to quantify *in situ* marine populations (Brock 1954, Harvey et al. 2002, Watson et al. 2005, Cole et al. 2007). It is cheaper relative to trawl surveys and is a more efficient way to monitor marine communities than extractive (Bellwood and Alcala 1988) and tag and recapture techniques (Watson and Quinn 1997, Stewart and Beukers 2000). This

method is commonly used to monitor fish communities in fragile marine ecosystems, such as coral reefs and MPAs (Bell et al. 1985, Kulbicki 1998, Harvey et al. 2001a, Cole et al. 2007). UVC methods can be broadly categorised into transect or point census techniques. Transect studies involve a diver moving along a predetermined line, recording the number of individuals of each species observed on either side. A diver undertaking the stationary point census will count all individuals in an area, defined by a quadrat or a physical feature, such as a reef patch. The counts generated from UVC surveys provide information on the abundance, density and species composition of the fish community (Bellwood and Alcala 1988, Cappo et al. 2007, Harvey et al. 2007a, Stobart et al. 2007) as well as habitat use and aspects of *in situ* behaviour. Basic length estimation also provides data on population size structure (Harvey and Shortis 1995, Harvey et al. 2001a).

A number of concerns regarding the accuracy of UVC results exist (Lincoln Smith 1988, Watson and Quinn 1997, Stobart et al. 2007). UVC have been found to underestimate fish abundance (Jennings et al. 1996, Harvey et al. 2002) due to poor counting, and difficulties in attempting to count multiple fish simultaneously (Harvey et al. 2002). The method is unsuitable for inconspicuous or camouflaged species which often go unnoticed (Kulbicki 1998, Stewart and Beukers 2000), and so rarely records all fish in the area. It is also difficult to standardise the method for inter-observer variability and this can cause significant biases. Biases have been identified in the estimation of fish length underwater (Bell et al. 1985) and the under and over estimation of counts (Williams et al. 2006). The marine environment imposes physical and physiological restrictions on the diver and limits the depth and time of surveys (Shortis and Harvey 1998, Harvey et al. 2001a, Stobart et al. 2007). The movement and speed of the fish in the divers' fields of view can also impact on the numbers of fish observed (Thresher and Gunn 1986, Lincoln Smith 1988, Watson and Quinn 1997) and however slow the observer swims they were unlikely to see and count all species (Lincoln Smith 1988).

The behaviour of some species towards the diver may also impact upon estimates (Jennings et al. 1996, Kulbicki 1998). Some fish species have also been observed to respond to the diver (Watson et al. 2005, Langlois 2006, Cappo et al. 2007). For example some species are cryptic or shy fish and are often rarely recorded, while some bolder, more conspicuous species are all counted (or even re-counted if they leave and return to a survey area) (Kulbicki 1998, Willis and Babcock 2000, Watson et al. 2005, Harvey et al. 2007a). When using open circuit SCUBA the noise and bubbles from the divers' apparatus also

affects the behaviour of fish, by causing either attraction (Chapman et al. 1974) or avoidance (Cole et al. 2007).

Divers' estimates of fish size often lack precision and accuracy which limits statistical power to identify differences in the population size frequency distribution (Harvey and Shortis 1995, Kulbicki 1998, Shortis and Harvey 1998, Harvey et al. 2001a, 2002, Watson et al. 2005). Errors in size estimation have been found to increase with fish size (Kulbicki 1998), so small inaccuracies in the measurement of larger fish can have a significant impact on the predictions of fish stock biomass (Bellwood and Alcala 1988).

More accurate estimates of fish size may be obtained from measurements from cameras. These can be mounted on remotely operated vehicles (ROVs) using lasers projected into the field of view to provide a grid at a known scale (Barker et al. 2001, Rochet et al. 2006). However, the movement and orientation of fish can cause errors in paired laser methods as objects must be at right angles to the laser for accurate measurement (Trenkel and Lorange 2005, Barker et al. 2001, Rochet et al. 2006). Camera systems carried by divers can also be equipped with paired lasers set at a known distance apart, such as the system used to document the recovery of Nassau groupers (*Epinephelus striatus*) in the Cayman Islands (Heppell et al. 2012). Laser systems are an improvement on visual length estimations but still suffer from the limitations of diver transects (Heppell et al. 2012). Fish abundance estimates made using ROVs can also be biased depending on whether the fish shows a positive or negative response (Stoner et al. 2008).

1.6.2.5. Surveys Using Underwater Camera Systems

As the reliability, performance and cost of digital camera technology has improved, underwater camera systems have become popular in marine monitoring (Willis and Babcock 2000, Harvey et al. 2007a, Stobart et al. 2007, Watson et al. 2009, Lowry et al. 2011). Autonomous cameras are valuable in monitoring fragile and protected marine communities as they remove the impact of divers on fish behaviour and the damage associated with extraction methods (Cappo et al. 2004, Cappo et al. 2007). Camera systems also create a permanent record that can be reanalysed to examine additional aspects, such as behaviour and size (Harvey et al. 2001a, Cappo et al. 2007, Stobart et al. 2007) and to train new observers (Cappo et al. 2007). Autonomous or remote camera systems can also be deployed to greater depths and into a wider range of environmental conditions than a diver, allowing a wider range of marine habitats and populations to be

surveyed (Willis and Babcock 2000, Cappelletti et al. 2007, Harvey et al. 2007a, Stobart et al. 2007, Jamieson et al. 2012). Remote systems also require less man and field time (Willis and Babcock 2000, Watson et al. 2005) reducing survey costs (Watson et al. 2005). The deployment time of underwater camera systems is primarily constrained by the battery life of the cameras and lights (Lowry et al. 2011) therefore removing the time constraints experienced by a diver. BUC systems can therefore be operated over long periods of time such as in the systems described in Lowry et al. 2011, that recorded for over 12 hours, and in Jury et al. 2002 that recorded the arrival patterns of lobster (*Homarus americanus*) in a baited trap for 24 hours.

1.7. Baited Underwater Cameras

Baited underwater cameras (BUC) systems disperse an odour plume into the surrounding areas which fish use to locate the bait. Those reaching and feeding on the bait are captured by a camera, providing information on the species, numbers, arrival times and behaviour of individuals attracted to the system. This raw data is used to make inferences about the wider fish communities in the deployment area (Priede and Merrett 1996, Bassett and Montgomery 2011). BUC systems can be tethered or autonomous. Tethered systems remain attached to the vessel and use a power supply allowing longer deployments (Lowry et al. 2011) and are a common option to examine slow moving and highly dispersed deep-sea communities which require long deployments (>12 hours) (Bailey et al. 2007).

The introduction of bait to an underwater camera system attracts at least some cryptic species (Stewart and Beukers 2000) and large ambush predators (Kruschel and Schultz 2012) rarely observed in unbaited camera or UVC surveys. This helps reduce the underestimation of cryptic fish and overcomes the issue of low fish counts in non-baited camera systems (Stewart and Beukers 2000, Lowry et al. 2011). Baiting is also an effective and cheap way to sample fish populations across a larger area (Bailey et al. 2007). The area of bait dispersal and thus the sample area has only been estimated for some BUC studies. In a shallow temperate reef system in New Zealand it was calculated that a bait plume with a radius of 10 m would sample an area of 314 m² compared to 125 m² recorded by UVC surveys in the same area. However, it was proposed that this area is likely to be larger with the effects of advection and turbulent diffusion (Willis et al. 2000). Also a circle represents an unrealistic odour plume shape as plumes will not spread uniformly in all directions and form an elliptical plume in the current direction (Sainte-

Marie and Hargrave 1987). The use of bait has been found to attract a greater number of individuals and species to the camera (Willis et al. 2000, Harvey et al. 2007a). The increased attraction of carnivorous fish to the BUC makes it less likely to produce low or zero abundance estimates for these species allowing for more statistical powerful relative comparisons (Willis et al. 2000, Wills and Babcock, 2000, Stoner et al. 2008).

The characteristics of the bait, such as the persistence and moisture contact, used in a BUC system will influence the area covered by the bait plume and its concentration or persistence (Dorman et al. 2012). This will influence the number and species of fish able to detect the plume and approach the cameras system. Previous studies using fish traps (Whitelaw et al. 1991) or longlines (Lowry et al. 2006) found that the type of bait used had a significant impact upon the abundance and composition of fish assemblages caught. Detailed studies of the effect of bait type on the species assemblages recorded by BRUVS have been carried out by Wraith, 2007 and by Dorman et al. 2012. Both studies concluded that the type of bait significantly influences the abundance and assemblage composition of reef fish observed by the BRUV and that pilchards (*Sardinops sagax*) was the most appropriate bait to use for BRUV studies. Compared to the other baits used (catfood, falafel mix and no bait) the use of pilchards resulted in less variation among samples, a greater similarity in the assemblages recorded between replicates and generated higher mean numbers of fish at each site (Dorman et al. 2012). Pilchards (*S. sagax*) (Watson et al. 2007, 2009, 2010, Langlois et al. 2012a, b, Harvey et al. 2002, 2007a) or (*S. neopilchardus*) (Willis et al. 2000, 2003) or other oily fish, such as mackerel (*Scrombus spp.*) (King et al. 2006, 2008), have been used almost exclusively in other BUC studies. For comparisons between BUC studies it is important that bait is standardised (Dorman et al. 2012).

1.7.1. Baited Underwater Cameras in the Deep Water Environment

BUC were initially developed to sample abyssal marine species (Isaacs and Schwartzlose 1982). A variety of baited video camera and recording systems have been used as part of the deep-sea exploration programme of Oceanlab, University of Aberdeen, and Scripps Institution of Oceanography, University of California, San Diego, to study abyssal scavenger communities (Bailey et al. 2007). These landers are autonomous units anchored to the sea floor (Priede et al. 1994, Smith et al. 1997), by a disposable ballast system which is released allowing the unit to surface following an acoustic command (Armstrong et al.

1992, Priede et al. 1994, Jones et al. 2003). The bait is placed in the camera field of view (Lampitt et al. 1983, Wilson and Smith 1984, Priede et al. 1990, Premke et al. 2006). Designs include the Free Vehicle Video (FVV), the Aberdeen University Deep Ocean Submersible (AUDOS) (Armstrong et al. 1992, Bagley et al. 1994, Priede et al. 1994, Priede and Merrett 1996, Smith et al. 1997, Priede and Merrett 1998, Collins et al. 1999, Yau et al. 2001, Jones et al. 2003) and the RObust BIOdiversity lander (ROBIO)(King et al. 2006, King et al. 2008).

Estimating the abundance of abyssal species is difficult and trawling uses extremely large amounts of ship time and requires very large, specialised winches (Priede and Merrett 1996, 1998). Fish brought to the surface die under the pressure and temperature changes, making tagging and laboratory studies impractical (Bailey and Priede 2002, Haedrich et al. 2002, Bailey et al. 2003). This has led to the exploration of remote sensing techniques to monitor the abyssal environment. Remotely Operated Vehicles transect studies in the deep-sea have similar problems of fish attraction and avoidance as shallow water UVCs (Trenkel et al. 2004). Static deep-sea baited underwater video cameras or autonomous landers have therefore been used to explore the deep-sea environments and communities (Priede and Merrett 1998, Bailey et al. 2007). BUCs overcome many of the problems of visual surveys and trawling and represent an effective way to study the abundance, behaviour, ecology and metabolism of deep-sea communities (Priede and Merrett 1996, 1998, Bailey and Priede 2002, Bailey et al. 2007). They have been useful in investigating marine communities in rough habitats where trawling was impractical (Priede and Merrett 1996, Jamieson et al. 2006, King et al. 2006, King et al. 2008) and to sample species previously poorly recorded by trawl surveys (Jones et al. 2003, Kemp et al. 2008).

Food falls are relatively rare in the abyss (Wilson and Smith 1984, Priede and Bagley 2000) and it is essential for the scavengers that rely on them to locate and consume them quickly (Wilson and Smith 1984, Armstrong et al. 1992, Smith et al. 1997). Abyssal scavengers have evolved the ability to quickly sense the fall of carrion from a great distance with highly sensitive chemoreception (Britton and Morton 1994), vision and olfactory senses (Bailey et al. 2007). Mobile scavengers play an important role in distributing food fall material throughout the deep-sea habitat where it can be used throughout abyssal communities (Armstrong et al. 1992, Collins et al. 1999). It is extremely difficult to observe a natural food fall occurring in this environment and this is overcome by the provision of a artificial bait via BUC systems (Wilson and Smith 1984).

The method congregates scavenger species, which are generally highly mobile and of a low density, to produce count and diversity data with less zeros and a reduced variance that improves the statistical power to detect spatial differences in population structure (Wilson and Smith 1984, Harvey et al. 2007a). This allows BUC systems to detect changes in scavenger populations with a reduced sampling effort (Malcolm et al. 2007) and less time and costs than deep-sea trawl surveys (Priede et al. 1994, Priede and Merrett 1996, Bailey and Priede 2002).

1.7.2. Baited Underwater Cameras in the Shallow Water Environment

BUC systems have been introduced to the shallow water environment to monitor the relative densities and species diversity of fish assemblages (Denny et al. 2004, Watson et al. 2005, Cappo et al. 2007, Heagney et al. 2007, Malcolm et al. 2007, Stobart et al. 2007, Gomelyuk 2009). Data from BUC studies have been used to investigate the distribution of fish numbers and species across a variety of gradients, including depth (Jones et al. 2003, King et al. 2006), seasons and regions (Jones et al. 2003).

1.7.2.1. Baited Underwater Cameras in Shallow Tropical Waters

BUC systems are increasingly popular as a method to monitor the diversity of reef fish in relation to the establishment of MPAs (Bond et al. 2012). BUCs is used a general term to describe all baited underwater camera systems. The Baited Remote Underwater Videos Stations (BRUVS) is a specific design of BUC developed at the University of Western Australia and has dominated BUC based research in the tropical environment. BRUVS are commonly deployed in pairs to form a stereo system which has been developed to allow accurate and precise measurements to be made of marine organisms (Harvey and Shortis 1995, Harvey et al. 2001a). This technique gives depth perception and allows the position of objects within a three dimensional space to be found (Harvey and Shortis 1995). The stereo-BRUV is able to generate length data with precision and accuracy only previously achievable using extractive methods and has been recommended to monitor fish assemblages and the effects of fishing pressures (Watson et al. 2005, Watson et al. 2009). Knowing the size or length of fish present allows fish biomass estimates to be made and can provide useful information for stock assessment (Harvey and Shortis 1995, Harvey and Shortis 1998, Harvey et al. 2001b). Fisheries managers set minimum legal catch sizes allowing a proportion of the fish to reach sexual maturity to produce recruits back into the

population (Watson et al. 2005, Watson et al. 2009). Length data from BRUVS can help to determine which proportion of the populations have reached maturity and the populations' ability to persist under current fishing pressures (Watson et al. 2009).

BRUVS have been primarily used in areas where measures have been implemented to reduce fishing pressures on the West Coast of Australia (Harvey et al. 2012), East (Cappo et al. 2004, 2007, Malcolm et al. 2007) and North (Gomelyuk et al. 2009). Several studies have compared the relative abundance of commercial and recreationally targeted fish populations between protected and non-protected areas. BRUVS have been used to study the impact of the protection status of the Houtman Abrolhos Islands (Watson et al. 2007, 2009) and Ningaloo Marine Park (Watson et al. 2010), Western Australia, on fish assemblages since their establishment. At both areas protection has had a positive effect on fish assemblages. However, recent BRUVS studies have found that the coral reef fish assemblages in the protected areas of the Houtman Abrolhos Islands, Western Australia, were not significantly different from those in areas open to fishing (Dorman et al. 2012), even for species previously observed to have relatively large populations in closed areas (McLean et al. 2010). BRUVS have also been used to survey pelagic and mid-water fish assemblages in Lord Howe Island Marine Park, Eastern Australia, where current speed was found to have a significant impact on the assemblages observed (Heagney et al. 2007). BRUV surveys have also been found to effectively survey commercially important fish assemblages in estuaries (Gladstone et al. 2012) and have been expanded to provide relative abundance estimates of elasmobranchs (Bond et al. 2012) and crustaceans (Jones et al. 2003). The system observes fish feeding at the bait from a horizontal orientation for 1 hour and once analysed, videos provide information on arrival times, species, counts and sizes. The assemblages observed by BRUVS have been compared to those collected near-simultaneously using other methods such as; UVC (Langlois 2006, Colton and Swearer 2010), traps (Harvey et al. 2012), longlines (Brooks et al. 2011), ROVs (Dunstan et al. 2011) and trawling (Cappo et al. 2004). BRUVS are considered an effective alternative to estimate the relative abundances and species richness of large, mobile species with reduced costs and time (Watson et al. 2005). Comparisons with other studies have highlighted that the ability to detect species is the greatest source of variability between techniques and that this is determined by the species' behaviour, size and crypsis (Lowry et al. 2011). BUCs efficiently sample mobile, ambush and cryptic predators that have specialist olfactory capabilities to enable them to locate the bait (Bassett and Montgomery 2011, Kruschel and Schultz 2012). Reef predators such as fish of the family Sparidae (Lowry et al. 2011),

Lethrinus, Serranidae (Harvey et al. 2012), moray eels, sharks and rays (Cappo et al. 2004) were observed more often and at larger sizes in BRUVS than in other methods. Many MPAs are primarily designed to protect these groups as they are often fisheries targets and therefore known to be vulnerable to human exploitation (Sadovy de Mitcheson et al. 2012). Large predators also act as indicators of the health of the wider reef ecosystem (Sergio et al. 2008) and data on these species and the impact of MPAs is vital to inform further management decisions. BRUVS have been used to study the reef fish and elasmobranchs (Cappo et al. 2007, Bond et al. 2012) communities across depth gradients and protection status in several tropical MPAs (Westera et al. 2003, Malcolm et al. 2007, Goetze et al. 2011).

1.7.2.2. Baited Underwater Cameras in Temperate Coastal Waters

One of the earliest uses of BUCs in the shallow water environment was developed by Willis and Babcock (2000) to investigate the effect of MPAs on shallow reef fish in New Zealand (Babcock et al. 1999, Willis and Babcock 2000, Willis et al. 2000, Willis and Anderson 2003, Denny et al. 2004, Willis and Millar 2005). The system consists of a single vertical high resolution colour camera in a waterproof housing attached to a light stainless steel frame with a triangular base centred on a bait (Willis and Anderson 2003, Willis et al. 2003, Denny et al. 2004). The unit was tethered to an anchored boat and deployed for 30 minutes and has documented the recovery of recreationally important pink snappers (*Pagrus auratus*) and blue cod (*Parapercis colias*) within the MPA network (Babcock et al. 1999, Willis and Babcock 2000, Willis et al. 2000, Denny et al. 2004). A mid-water BRUV system was also developed to survey the pelagic fish fauna of the temperate reefs of Eastern Australia and highlighted the importance of currents on the fish assemblages observed (Heagney et al. 2007). Studies of the potential application of BUCs in sub-tropical rocky reef-habitats have indicated that the system generated accurate estimates of species richness but more information on behavioural responses to the bait were required for true abundance estimates to be generated (Stobart et al. 2007).

1.7.2.3. Baited Underwater Cameras in Shallow Polar Waters

The success of BUCs to examine scavenger and predatory assemblages in lower latitudes has prompted BUC studies of scavengers in high latitude sites (Premke et al. 2006, Smale et al. 2007c). The AUDOS system was used to estimate the abundance of the

commercially exploited deep-water Patagonian toothfish (*Dissostichus eleginoides*) in relation to long-line fishing around South Georgia and the Falkland Islands (Collins et al. 1999). Data on the species distribution, biology and ecology has been collected via fishery catch and effort data, however, the variability in data from different vessels made it difficult to interpret (Yau et al. 2001). Additional information is essential as the exploitation of the fishery began with sparse information on the toothfish population dynamics and its ability to withstand fishing pressures (Collins et al. 1999, Yau et al. 2001). Fishing is prohibited around the Antarctic mainland but the impact of iceberg scour on the shallow marine ecosystems is a major disturbing force to marine communities and provides large masses of carrion that scavengers exploit. A BUC system investigated the impact of iceberg scour on scavenger biodiversity and distribution throughout the summer and winter on the Antarctic Peninsula and found that scavenger assemblages and bait consumption rates varied between areas experiencing different ice disturbance regimes (Smale et al. 2007c).

1.7.3. Baited Underwater Camera Data Analysis Methods

1.7.3.1. Abundance and Diversity

The number and diversity of fish present at the BUC system at any one time, in both the abyssal and shallow habitat, is influenced by an array of factors (Bailey and Priede 2002). The area covered by the dispersing bait plume is dependent upon the current speed and direction, as well the depth and topography of the environment (Sainte-Marie and Hargrave 1987, Watson et al. 2009). The area of the plume detected by scavengers is dependent upon the gradient of decay, determined by the bait characteristics (Bailey and Priede 2002, Harvey et al. 2007a) and the olfactory capabilities of the fish (Sainte-Marie and Hargrave 1987). The fish available to detect the plume will be governed by the number in the effective area (abundance) and the time of these individuals arriving at the BUC system will be influenced by their through water swimming speed (Priede and Merrett 1996, Bailey and Priede 2002). The energy expended on exploiting a food source is defined by Charnov's marginal value theorem of optimal foraging (Cappo et al. 2004) that states that the rate of energy acquisition from a resource patch will diminish with time and that an optimal staying time at a food patch exists. Staying time depends upon when the rate of energy extraction at the patch drops below the average rate for the whole system (Priede et al. 1990). Therefore the staying time of individuals is an indicator of

the resources available within that environment (Priede and Merrett 1998, King et al. 2006) and will reflect the satiation state and response of the fish to the bait plume. Interactions with conspecifics will affect an individual fish's perception of the value of the bait and its decision as to whether to approach or remain (Thurston et al. 1995, Cappelletti et al. 2004).

The arrival process of the deep sea grenadier *Coryphaenoides armatus* at a BUC was modelled using an inverse square relationship:

$$N = C/t_{arr}^2$$

where N is the number of fish per square kilometre and C is a constant, dependent upon the current velocity and through water fish swimming speed towards the BUC system (Priede et al. 1990, Priede and Bagley 2000). For *C. armatus*, C was estimated to equal 5.333×10^8 when bottom currents and fish through-water swimming speed were both 0.05 ms^{-1} , speeds commonly observed in the northern hemisphere abyssal environment (Priede et al. 1990). t_{arr} represents the time elapsed between the beginning of the camera deployment and the arrival of the first fish. The model was developed by Priede et al. (1990) to allow scavenger density to be estimated from their arrival rates at the BUC in conjunction with information on the bait plume dynamics, current velocities and fish swimming speed. Arrival rates are of interest as a bait placed amongst an abundant scavenger population has a greater chance of being reached by an individual quickly (Bassett and Montgomery 2011). Priede and Merrett, (1998) found that scavenger densities generated from this relationship, when both current speed and through water fish swimming speed equal 0.05 ms^{-1} , correlated well with abundance estimates from independent trawling surveys in the North Atlantic.

The relationship:

$$N_t = \alpha_0/x \cdot e^{-xt} (e^{\beta t} - 1) \quad \text{if } t > \beta$$

$$N_t = \alpha_0/x(1 - e^{-xt}) \quad \text{if } t \leq \beta$$

where N_t is the number of fish present in the camera field of view at time (t) (minutes) after the BUC reaches the sea floor, α_0 is the initial arrival rate of fish at time zero (fish per minute) to the BUC and β is the mean fish staying time (minutes) and x is a constant

describing the decay of the odour plume estimated from dilution and consumption effects. α_0 is found by fitting a slope to the arrival data and β corresponds to the time to reach maximum fish numbers and is calculated using the relationship:

$$N_{\beta} = \alpha_0 / x (1 - e^{-\beta x})$$

Measures of β and α_0 are used to find the best fit of x . The model was fitted to the maximum number of *C. armatus* recorded every 30 minutes by BUC systems in the Porcupine and Madeira Abyssal Plains (Priede et al. 1990, King et al. 2006).

Assumptions, based around the dynamics of the bait plume and the way in which fish interact with it are incorporated into the models. However, if incorrect, they can introduce bias. The model of Priede et al. (1990) assumes that fish are static prior to the detection of the odour plume. However, it is difficult to know if this is correct as fish are not viewed prior to reaching the bait. Bailey and Priede (2002) developed models to describe bait use by scavengers that use an active cross current, sit and wait, or a passive drifting foraging strategy. Out of the three models, arrival times from the cross current model fitted best with trawl data and patterns of fish arrival but described peak fish numbers greater than observed in field data. The sit and wait model described peak fish numbers more accurately than the cross current model but the pattern of arrivals fitted poorly with trawl data (Bailey and Priede 2002).

A further examination of modelling processes to estimate scavenger fish abundance found that arrival times do not accurately predict the abundance of *C. armatus*. Priede et al.'s 1990 models use a deterministic approach where the model outputs are determined by known relationships. Using this approach there is no random variation incorporated into the models and with a given input the model will always give the same output. However, fish arrival times have a high variance and the use of deterministic modelling, such as in the Priede et al. 1990 model, prevents uncertainty being quantified (Farnsworth et al. 2007). Farnsworth et al. 2007 therefore developed a model of the pattern of fish arriving at the bait, until the maximum number were reached, using a Poisson regression model that incorporated the stochastically (randomly) distributed variables of attraction and departure rate. In this study the stochastic modelling approach provided the most precise measure of scavenger abundance (Yau et al. 2001, Farnsworth et al. 2007). However, the Farnsworth models have not been adopted by camera users, partly due to their complexity but also

because of the large number of parameter estimates needed compared to the models by Priede et al.

Almost all shallow-water baited underwater camera studies have used MAX_N , the maximum number of individuals present in the camera field of view at one time, to generate estimates of relative abundance. The measure allows comparisons to be drawn between fish assemblages at different sites, habitats and protected/adjacent non-protected areas (Willis et al. 2000, Colton and Swearer 2010). However, this measure does not reflect the detailed interactions between individuals and the bait odour plume (Stobart et al. 2007, Colton and Swearer 2010) or the succession of different fish species and sizes visiting the system (Harvey et al. 2012). For a measure of abundance that can be compared across methods, time and locations, the area of the odour plume that attracts individuals to the camera must be found. This will require measurements on both the dispersal dynamics of the bait plume and the behaviours of the fish in relation to the plume (Farnsworth et al. 2007, Colton and Swearer 2010).

1.8. Conclusion

In conclusion, BUCs have a bright future in providing information on fish communities to enable the evaluation of management practices to conserve marine biodiversity, particularly within marine protected areas. The method enables necessary data to be gathered on species valuable to both the function of marine ecosystems and commercial fisheries in a non-destructive and cost efficient manner. However, the method requires improvement if it is to be of maximum usefulness. Areas of uncertainty remain in the application of BUCs in temperate and polar regions, especially where water clarity is lower and currents faster than in either tropical or deep water systems. Present methods of BUC data analysis are not sufficient to make best use of the large datasets being produced as the use of the BUC method increases.

1.9. Thesis Aims and Objectives

This thesis sets out methods developed to use BUCs in temperate, tropical and polar environments and their application to biological questions concerning the factors controlling shallow water marine biodiversity and abundance. During these studies data was collected for the development of a new model system for the generation of absolute fish abundances from BUC data.

Chapter 2: The objective of the work in Chapter 2 was to describe the design and development of a BUC system and deployment procedure suitable for attracting, identifying and counting temperate fish and invertebrate species. This work was carried out in the temperate waters on the West coast of Scotland. The development of BUC systems has been limited in temperate waters and a cost- and - time efficient BUC methods would be valuable to monitor the before and after impact of marine protected areas proposed in Scottish inshore waters. The ultimate objective for the method is to collect data on the diversity and relative and absolute abundance of fish and crustacean assemblages.

The ability of the BUC system to gather data to enable relative comparisons of fish and crustacean assemblages was demonstrated using a study comparing the diversity and abundance of assemblages recorded between sites of different protection status on the West Coast of Scotland.

It was hypothesised that 1) the BUC system would be able to attract and provide data on the diversity and abundance of fish and invertebrates assemblages and 2) that the assemblages would be significantly different between sites.

Chapter 3: The fish assemblages of the tropical coral reef system of the Gulf of Aqaba are distinct from those observed in other regions, making this an area of conservation importance. Here UVC surveys by SCUBA diving have been predominately used to gather data on shallow water coral reef fish assemblages. However, with this method it has been difficult to obtain frequent surveys due to the high cost involved and it was proposed that BUCs could represent an efficient additional survey method that would enable data to be gathered more frequently on coral reef fish assemblages.

The objective of this study was to design and implement a BUC system in the coral reef environment of the Gulf of Aqaba from which data could be gathered on the species and relative and absolute abundance of predatory fish species. The ability of the BUC method to survey the coral reef fish assemblage was compared to corresponding UVC surveys conducted in the same location and at approximately similar time periods.

It was hypothesised that 1) the BUC surveys would observed a greater diversity and abundance of predatory fish species than the corresponding UVC surveys due to behavioural aspects favouring detection in the BUC and 2) that this would enable BUCs to survey predatory species using a smaller number of surveys.

Chapter 4: The two objectives of this study were to use the BUC system to gather data 1) to investigate how scavenger behaviour, distribution and abundance varied between high and low iceberg scour impact conditions at 4 sites and 3 depths Ryder Bay, Adelaide Island, Western Antarctic Peninsula, using a novel BUC system.

The hypotheses relating to these objectives are that 1) the pattern of scavenger richness and abundance across the depth gradient will vary significantly between the high and low scouring impact conditions and sites, 2) individual scavenger species abundance will vary according to their adaptation to either high or low scour conditions.

Chapter 5: The two objectives of this study were 1) to develop a stochastic modelling approach to enable the estimation of absolute abundance of fish and invertebrates using arrival data collected using a shallow water BUC system and 2) the generation of absolute abundance estimates from BUC data collected in the temperate, tropical and Antarctic marine environments.

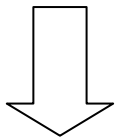
The hypothesis related to these objectives were that 1) the models developed using in-situ measurements of current speed and fish swimming speed would generate abundance estimate that were similar to those from corresponding UVC surveys and 2) that the model would produce abundance estimate that were comparable to those generated by the corresponding UVC surveys.

1.10. Thesis content flowchart

Title, Abbreviations, Contents, List of Figures, List of Tables

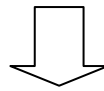
Abstract

Development of a BUC system for attracting, identifying and counting fish and invertebrate species for the temperate, tropical and Antarctic environments.



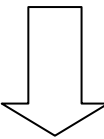
Chapter 2: Temperate

Demonstrate the ability of the BUC to investigate the relative abundance of invertebrate and fish assemblages between different sites on the West coast of Scotland.



Chapter 3: Tropical

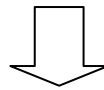
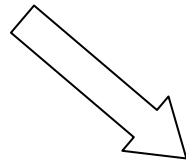
Tests the ability of the BUC method to survey predatory coral reef fish assemblage in the Gulf of Aqaba compared to corresponding UVC surveys.



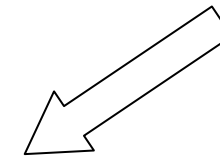
Chapter 4: Antarctica

Investigates how scavenger behaviour, distribution and abundance varied between sites and depths with different iceberg scouring frequency.

Data generated used to develop models.



Chapter 5: Modelling methodology



Development of a stochastic modelling approach to enable the estimation of absolute abundance of fish and invertebrates using arrival data collected using the BUC system and demonstrated how absolute abundance estimates can be generated from BUC data collected in the temperate, tropical and Antarctic environments.

Final Discussion

2. Chapter 2

Development of a low-cost baited underwater camera survey method for UK coastal marine systems and its application to a “no take zone” and two open areas in the Firth of Clyde, Scotland

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2.1. Abstract

The deployment of baited underwater cameras is an increasingly popular method for the monitoring of marine systems, in particular for the closed areas where there is a need to minimise seabed impacts. Here the design and development of a baited underwater camera system suitable for attracting, identifying and counting temperate shallow water (< 30 m) fish and crustacean species on the West coast of Scotland is described. The use of BUC systems has been limited in temperate waters and a cost-and-time efficient method could be valuable to monitor the before and after impact of the proposed Scottish Marine Protected Area network. As a test of the BUC, deployments were made in Lamlash Bay no-take zone (n = 6) and in two control open sites (n = 8 and n = 8) at the same depth (15 m \pm 3.5 m) in May/June 2010. The maximum number of individuals observed in the camera field of view in a single image (Max_N) of each fish and crustacean species in each deployment was recorded as was the time to the first arrival (t_{arrival}) and the time to reach Max_N (t_{MaxN}) to provide relative abundance estimates between the no-take zone and the two control areas. As well as providing a test of the baited underwater camera these data provide baseline data early in the life of the no-take-zone against which future baited underwater camera studies can be compared.

2.2. Introduction

Monitoring can be defined as “the process of gathering information about some system’s state variables for the purpose of assessing system state and its change over time” (Yoccoz et al. 2001). State variables are those describing an attribute of the system against which its status can be measured and those chosen will depend upon the aims of the monitoring programme. In the context of monitoring marine populations and communities such variables could include population abundance, structure and biodiversity (Katsanevakis et al. 2012). Monitoring in the marine environment is important to provide the information required to indicate whether management measures are proving effective (Day 2008 and Katsanevakis et al. 2011). Marine protected areas (MPAs) are becoming a common management measure in the conservation of marine environments and communities (Halpern 2003).

International agreements have been made by the nations party to the Convention of Biological Diversity and at the World Summit of Sustainable Development to expand the global network of MPAs (Fox et al. 2012, Pita et al. 2013). MPAs are defined as "an area within the maritime area for which protective, conservation, restorative or precautionary measures, consistent with international law have been instituted for the purpose of protecting and conserving species, habitats, ecosystems or ecological processes of the marine environment" (OSPAR 2003). A number of types of MPAs exist that provide different degrees of protection (Sale et al. 2005). A no-take zone (NTZ) is a MPA where all forms of human exploitation are prohibited (Roberts and Hawkins 2000) and in 2006 represented 0.04 % of the world’s MPA’s (Jones 2006).

As well as providing a conservation benefit MPAs can also enable fish and crustacean populations to recover without the pressure of fisheries (Willis et al. 2003). It is important to document the change in fish and crustacean communities inside MPAs to enable their potential as a conservation tool to be gauged (Selig and Bruno 2010) and also to allow MPAs to act as a reference area, making it easier to separate fisheries effects from those of natural variability.

Monitoring is required to determine whether an MPA is achieving its management objectives. This is difficult for several reasons, in particular because of the difficulty of

finding suitable control areas. For example, few MPA sites are chosen at random, usually being either biological special and/or geographically convenient. Finding areas which are similar in all other respects other than differences in management may be difficult. Other factors include the lack of certainty before MPA implementation, preventing a time series being established before closure.

The effects of an MPA on the fauna of interest can be considered as the “impact” in the Before/After, Control/Impact (BACI) experimental design by Green, (1979). In a BACI design data must be collected at both the “impact” and “control” site at least once before the time of the disturbance and once after the disturbance (Smith et al. 1993). In a MPA context the impacted site would be the MPA and a non-protected site would be the control. The MPA would be considered to be having an impact if a change was detected in the impacted site and not the control. However, this design was considered to not be statistically vigorous and to represent pseudoreplication by Hulbert (1984).

Pseudoreplication is “the use of inferential statistics to test for treatment effects with data from experiments where either treatments are not replicated (though samples maybe)” (Hulbert 1984). The need for additional temporal replication to separate the effects of the MPA from the natural spatial and temporal fluctuations of populations were identified by Bernstein & Zalinski, (1983) and Stewart-Oaten et al. (1986). It was considered by these authors that with sampling at one point in time the potential to detect the impact would be low as it could be confounded by the natural cycle of the population and could not be directly linked to the impact. Monitoring the impacted site and one control site several times before the disturbance event and several times afterwards was suggested to overcome this solution (Bernstein and Zalinski 1983, Stewart-Oaten et al. 1986).

Stewart-Oaten et al. (1986) also highlighted that the BACI design using a single control location does not provide an appropriate test for the presence of an impact as there is a lack of spatial replication. An asymmetrical design using one impact site and multiple control sites overcomes the problem and allows population impacts to be detected using spatial replication (Underwood 1994). The design enables contrasts to be made between impacted and control locations and its interactions with time (Underwood 1994, Martin et al. 2012). Underwood, (1992) built upon this experimental design but also incorporated spatial replication by including multiple impacted and control sites, known as the beyond-BACI design. Ideally this would include replicated impacted and control sites, but the probability of having more than one impacted site at one time is unlikely but there is the possibility of using several similar but randomly chosen control sites.

Few studies have implemented Underwood's (1992) beyond-BACI design because there is often a lack of spatial and temporal data prior to the establishment of MPAs (Mitchell et al. 2005). The beyond-BACI design also assumes that the location of the MPA is randomly selected however, MPA locations are generally selected because they encompass a special species or habitat and can also be selected for social, economic and logistical reasons (Lincoln-Smith et al. 2006). This has led to debate over the suitability of the beyond-BACI methodology (Stewart-Oaten and Bence, 2001), yet beyond BACI and BACI designs have been applied in several MPA impact studies (Moland et al. 2013, Rife et al. 2013).

A meta-analysis of MPA impact studies between the 1970 and 2010 found that most were conducted in tropical and warm temperate Mediterranean waters and very few in cold temperate regions (Caveen et al. 2012). Within these temperate studies few have focused on the impact of MPAs on fish assemblages as the information on fish connectivity is limited in the temperate environment (Tobin et al. 2010).

MPA monitoring and studies of MPA effectiveness require methods which are not damaging to the features of interest. Data on inshore communities is generally obtained from fisheries landings and log books or from fisheries-independent trawl surveys (Harvey et al. 2012). The use of extractive techniques may be considered inappropriate within MPAs especially if fragile habitats may be damaged by their use (Cappo et al. 2004, Watson et al. 2005). A wide range of non-destructive tools are available including SCUBA surveys, drop down cameras and remotely operated vehicles. The deployment of baited underwater cameras (BUCs) is an increasingly popular method for the monitoring of MPAs and their utility has been compared with other, more established methods (Willis et al. 2000, Cappo et al. 2004, Watson et al. 2005, Colton and Swearer 2010) (for a review see Ch1). Unsurprisingly, BUCs are most useful for surveying scavenging and predatory species (Nickell and Moore 1992, Harvey et al. 2007a), and in many areas scavenging crustaceans and large predatory fish are the most important fisheries targets (Watson et al. 2009) and may also act as indicators of ecosystem health (Greenstreet et al. 2011, Shephard et al. 2011). BUCs have been used to monitor inshore fish and crustaceans in a number of temperate locations in New Zealand (Babcock et al. 1999, Willis and Babcock 2000, Willis et al. 2000, Willis and Anderson 2003, Denny et al. 2004, Willis and Millar 2005), Australia (Heagney et al. 2007) and the Mediterranean (Stobart et al. 2007) and are discussed in more detail in Chapter 1. However, the use of

BUCs in temperate shallow UK waters is limited to a few isolated studies (Howarth et al. 2012, Martinez et al. 2011, Nickell and Moore 1992). Martinez et al. 2011 used 27 replicate deployments at 100 m in the northern North Sea to make behavioural observations of fish species commonly observed at the bait; hagfish (*Myxine glutinosa*), dab (*Limanda limanda*), whiting (*Merlangius merlangus*) and haddock (*Melanogrammus aeglefinus*). Nickell and Moore (1992) used a BUC system in the Clyde Sea area to study scavenger behaviour and found that the bait was dominated by invertebrate scavengers. A recent scientific survey has involved the use of a baited underwater video system by researchers from the University of York and has compared fish and crustacean communities inside and outside the Lamlash Bay NTZ, Firth of Clyde, SW Scotland, between the 18th July and 25th August 2011 (Howarth et al. 2012).

Fisheries are implicated in reductions in fish biomass and landings in the Firth of Clyde (Thurstan and Roberts 2010). The inshore waters of the Clyde, on the West coast of Scotland, once supported fisheries for herring (*Clupea harengus*), cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*) and turbot (*Psetta maxima*), however, intensive bottom trawling has reduced fish stocks so only commercial fisheries for the Norway lobster (*Nephrops norvegicus*) and the scallops (*Pecten maximus* and *Aequipecten opercularis*) now exist (Thurstan and Roberts 2010, Heath and Speirs 2012). In 1889 a 380 square mile area in the Firth of Clyde was closed to bottom trawling due to concerns over the damage that it was causing to important fish nursery and spawning grounds. This regulation was combined with a Scotland wide ban in the same year on trawling within three-miles of the low-water mark. However, the Clyde area was re-opened in 1962 in response to declines in herring catches and the desire to utilise areas for the fishing of Norway lobster and the three-mile ban was removed in 1984 (Thurstan and Roberts 2010).

The fishery for Norway lobster employs both mobile otter trawls and static creels (Tuck et al. 1997, Thurstan and Roberts 2010). As well as trawls there is a fishery for king scallop (*Pecten maximus*), mainly conducted using dredging (Howarth et al. 2011). Dredging reworks the seabed removing infaunal (Eleftheriou and Robertson 1992) and epifaunal benthic communities from both sand and gravel sediments (Currie and Parry 1999, Boulcott and Howell 2011). Rocky reefs represent poor scallop fishing grounds and are avoided by scallop dredgers however, when impacted by accident they can remove epibenthic communities from rocky reefs (Boulcott and Howell 2011) and maerl

beds (Hall-Spencer and Moore 2000). Trawling also generates large volumes of discards; i.e. 9 kg of discards, primarily invertebrates and juvenile gadoids (haddock, cod and whiting (*Merlangius merlangus*) and flat fish for every 1 kg catch of Norway lobster (Bergmann and Moore 2001, Bergmann et al. 2002).

Under UK and Scottish legal systems areas of the seabed are closed to fishing, or the types of gears are restricted and further areas are affected by EU legislation such as the habitats and birds directives. The UK is under international and European wide agreements through the European Marine Strategy Framework Directive (MSFD) and the North-East Atlantic OSPAR Commission to expand its current network of MPAs (Jones and Carpenter 2009, Pita et al. 2013). In the Firth of Clyde this includes seasonal restrictions on bottom fishing to reduce impacts in a cod spawning area and since 2008 a NTZ in Lamlash Bay, Isle of Arran.

All sea fishing has been prohibited in the NTZ under the Inshore Fishing (Scotland) Act 1984 (Howarth et al. 2011, Pita et al. 2011). The NTZ is intended to allow the marine environment and shellfish and fish populations to regenerate and a recent surveys revealed that the abundance of juvenile scallop (*P. maximus*) and the size and age of adult scallops is higher within the NTZ and has been linked to a higher abundance of macroalgae in the NTZ (Howarth et al. 2011). Other scientific surveys have involved the use of baited remote underwater video and diver underwater visual census surveys by researchers from the University of York and have compared fish and crustacean communities inside and outside the NTZ between the 18th July and 25th August 2011.

2.3. Aims and Objectives

2.3.1. Objective 1

Objective 1 of this chapter was to describe the design and development of a BUC system and deployment procedure suitable for attracting, identifying and counting temperate shallow water (< 30 m) fish and invertebrate species on the West coast of Scotland. The development of BUC systems has been limited in temperate waters and a cost-and-time efficient method would be valuable to monitor the before and after impact of the MPA network proposed in Scottish inshore waters. The ultimate objective for the method is to collect data on the diversity and relative and absolute abundance of fish and crustacean

assemblages. Absolute abundance estimates are generated using the modelling methodology described in Chapter 5.

2.3.2. Objective 2

A second objective was to demonstrate the ability of the BUC system to gather data to enable relative comparisons of scavenging and predatory fish and crustacean assemblages between sites. This was done using a study comparing the relative diversity and abundance of fish and crustacean assemblages recorded between sites in the Firth of Clyde, West coast of Scotland. The NTZ Lamlash Bay was one of the three sites studied to potentially provide baseline data against which future BUC studies could be compared to monitor the impact of protection status on fish and crustacean species. This work represents the first BUC data collected in a UK MPA. It was hypothesised that the BUC system would be able to attract and provide data on the diversity and relative abundance of scavenging and predatory fish and crustaceans between these sites.

2.4. Material and Methods

2.4.1. Objective 1

2.4.1.1. *Baited Underwater Camera Equipment*

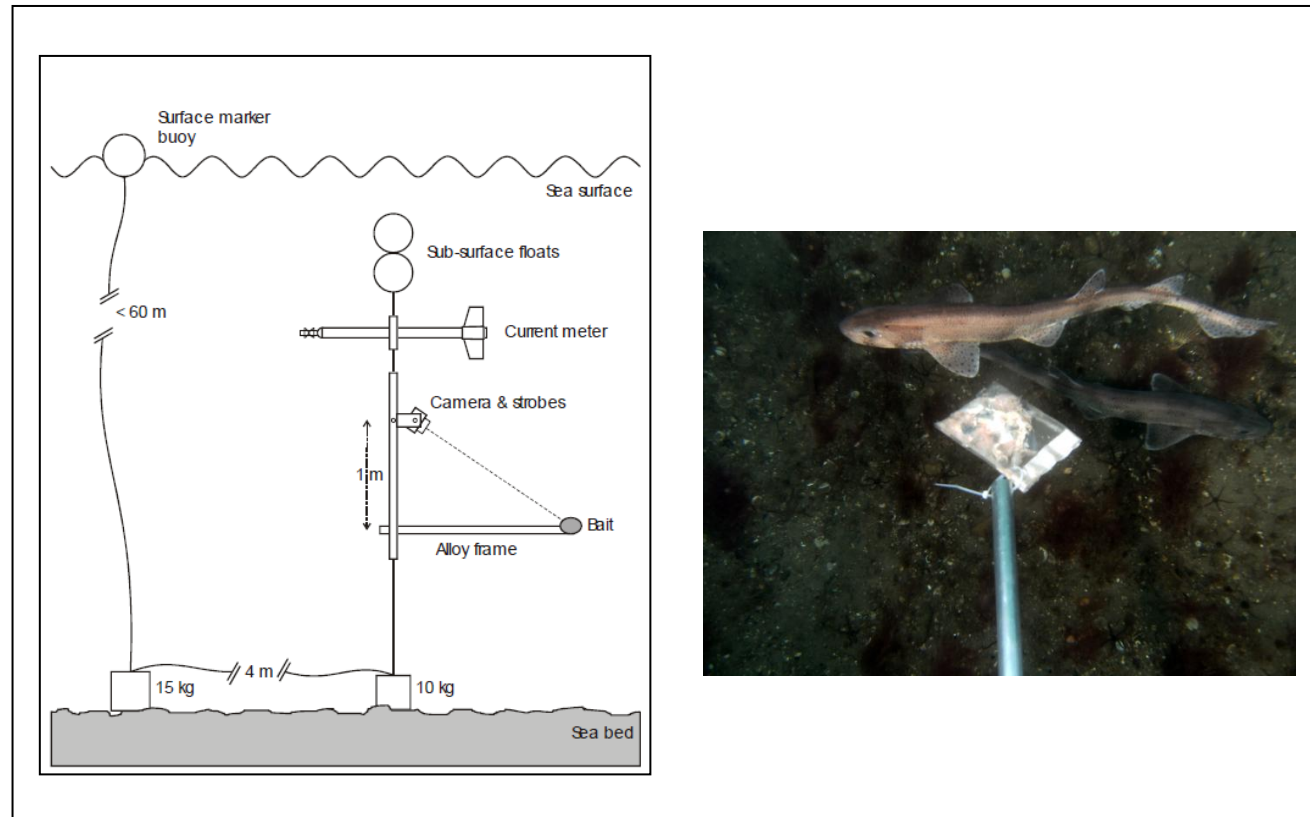
The BUC consisted of a digital camera (SeaLife DC800 or DC1000) enclosed in a SeaLife underwater housing synchronized, via optical cables, with two variable-power digital slave strobe light units (Epoque ES-23DS). The camera was placed in either time lapse mode (30 seconds intervals) or in video. The optimal camera settings and lighting positions for photography in West coast of Scotland waters were found following a series of test deployments under University Marine Biological Station, Millport's (UMBSM) Keppel Pier during March and April 2010.

2.4.1.2. *Deployment Equipment*

The camera equipment was supported on an L-shaped frame of aluminium tubing held together by key clamp fittings (Fig. 2.1). The u-shaped bracket holding the camera was bolted to the vertical element of the frame and was angled downwards at 60° to view the mesh bait bag attached to the far end of a horizontal pole. 200 g of chopped mackerel

(*Scomber scomber*) was used as bait. The strobes were attached to a horizontal pole and were positioned 50 cm on either side of the camera also at approximately a 60° downwards facing angle towards the bait. The frame was designed to provide adequate support and protection for the camera system, while minimising weight and the three-dimensional structure, which might affect fish behaviour (Jamieson et al. 2006). The key clamps and bracket enables the dimensions of the frame and the angle of the camera to be easily altered to suit different underwater conditions. For example, the distance of the camera and strobes from the bait could be reduced if using the system for a study in reduced visibility. When deployed from a boat, the camera frame was lowered on a J-shaped mooring and supported upright in the water column by two mid-water buoys and weighted by a 10 kg concrete block. This weight was also attached to a 15 kg block by a 2 m length of chain which was in turn attached to a surface buoy to avoid movement of the camera frame caused by motion of the marker buoy and buoy line. A variety of frame designs were deployed from Keppel Pier and the camera images examined afterwards to find an equipment configuration that produced the clearest images. A number of weighting and buoyage configurations were also tested until a design that would keep the frame and camera and lighting equipment upright and stable at the deployment position was found.

Figure 2.1. Systematic diagram of baited underwater camera equipment and mooring (Smith et al. 2010) and an image of a lesser spotted dogfish (*Scyliorhinus canicula*) in the Control 1 site on the 29th June 2010. The bait arm and the bait enclosed in a mesh bag can be seen in the BUC image.



2.4.1.3. Methodological Tests

Once the optimal camera settings and equipment positioning had been found 5 test deployments were made to collect data on the fish and crustacean species attracted to the BUC system. Analysis of these deployments aimed to find the deployment time that would encompass all species recorded to allow reliable between site comparisons of species richness. The maximum number of individuals seen in a single image (Max_N), the time to the arrival of the first individual (t_{arrival}) and the time at which this occurs (t_{Max_N}) were used as indices of fish and crustacean relative abundance. However, for Max_N , t_{arrival} and t_{Max_N} to be used to detect between site differences in fish and crustacean assemblages it is required that the BUC deployment time must be able to record all indices. This was tested by examining the time that Max_N , t_{arrival} and t_{Max_N} occurred in five x 180 min deployments. A similar procedure was followed during the development of a baited underwater video system in New Zealand (Willis and Babcock 2000).

2.4.1.4. Lighting Effect

The effect of the lights on a range of fish species (*Pollachius virens*, *Centrolabrus rupestris* and *Scyliorhinus canicula*) that approached the camera system were studied during the five test developments by viewing fish feeding at the bait with a separate video camera attached to the same frame (filming under ambient light). If the individual remained at the bait when the strobe fired the lighting would be considered appropriate.

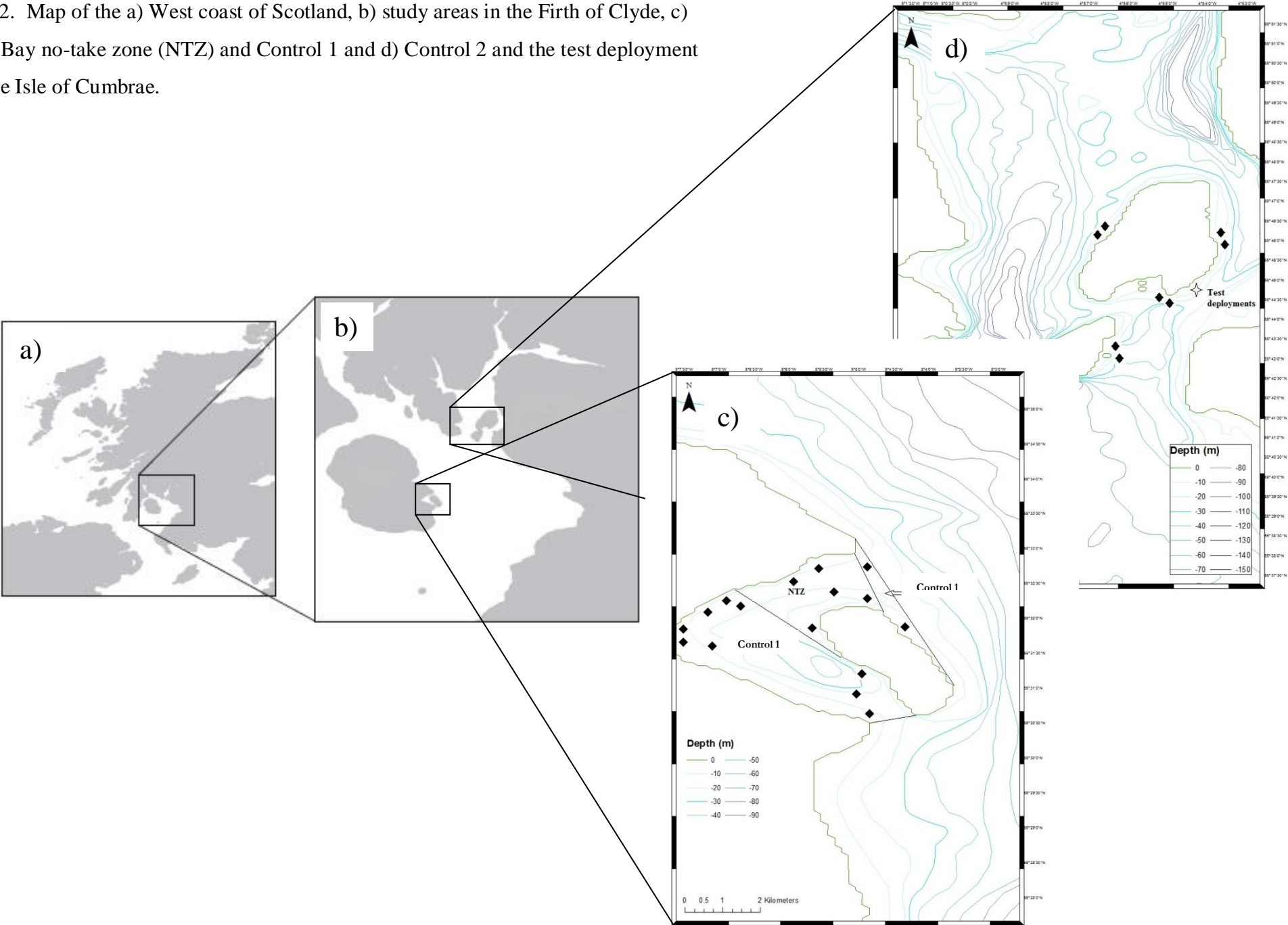
2.4.1.5. Test Deployment Details

Deployments were made from Keppel Pier, UMBSM, on the Isle of Cumbrae, Firth of Clyde, at a depth of between 4.8 and 6.2 m and lasted for 180 minutes between the 22nd April and the 3rd May 2010 (Fig. 2.2). 180 minutes was the limit of the camera battery power in the cold temperate waters. Deployments were at least 24 h apart and at the same tide state each day. This ensured that the bait plumes from previous deployments did not interfere with subsequent deployments and that current conditions were as similar as possible between deployments.

2.4.1.6. *Image and Data Analysis*

Images were viewed and edited in Adobe Photoshop CS6[®] to enhance the contrast and lighting to enable the species and number of individual crustaceans and fish in each image to be recorded. The arrival patterns for the four test deployments were analysed and showed in what deployment time period all species and the Max_N was recorded.

Figure 2.2. Map of the a) West coast of Scotland, b) study areas in the Firth of Clyde, c) Lamlash Bay no-take zone (NTZ) and Control 1 and d) Control 2 and the test deployment site by the Isle of Cumbrae.



2.4.2. *Objective 2*

2.4.2.1. *Deployment Equipment and Procedure*

The camera settings and equipment configuration used in this study were the optimal settings described in Objective 1 (2.5.1.1). In addition to the equipment and deployment procedure described in 2.4.1. time lapse images were recorded every 30 seconds and deployments latest for the time identified as encompassing all species and the Max_N in the results of Objective 1.

2.4.2.2. *Deployment Sites*

The NTZ encompasses a shallow inshore (0 – 29 m) area of 2.67 km² in Lamlash Bay, South East Arran, West coast Scotland, between the North end of Holy Island and the shores of Arran. The Isles of Cumbrae are located in the lower Firth of Clyde (Fig. 2.2). Three study sites were used within the Firth of Clyde. The impacted site was inside the Lamlash Bay NTZ and the controls sites were in the open areas adjacent on either side of the NTZ (max 1 km from the reserve boundary) (Control 1) while Control 2 was around the Isles of Great and “Wee” Cumbrae. Camera deployment positions at the three sites were from a random number generation from a range of possible positions at a depth of 15 m ± 3.5 m. Deployment times were organised via a rotational matrix which ensured that two deployments were not made consecutively in the same site. This also allowed bait plumes to disperse and for fish and crustaceans to resume their previous behaviours and distributions. The use of the matrix also ensured that all deployments at a particular site were not made at the same time of day. 6 deployments were made within the NTZ and 8 at both Control 1 and Control 2. Deployments in the NTZ and Control 1 were from the RV Aora, University Marine Biological Station Millport (UMBSM) and from the RV Actina, UMBSM, in Control 2. Deployments in Lamlash Bay were between the 28th and 29th June 2010 and those near the Isle of Cumbrae were between the 28th May and the 4th of June 2010. Deployment details are in Table 2.1 and marked on Fig. 2.2. Two BUC systems were used during this study and a current meter was attached to one of the systems enabling data on current speed and direction to be collected in 11 of the deployments (current meter data displayed in chapter 5).

Table 2.1. Details of baited camera deployments at Control 1 and Control 2 and Lamlash Bay no-take zone (NTZ), Firth of Clyde, West coast Scotland.

Site	GPS Position	Date	Start Time	Depth (m)	Duration (minutes)
Control 2	55 44.67N, 004 54.47W	28/05/2010	10:00	12.5	60
Control 2	55 43.12N, 004 56.24W	28/05/2010	11:45	15	60
Control 2	55 47 05N, 004 55.51W	28/05/2010	13:25	14	60
Control 2	55 43.12N, 004 56.24W	03/06/2010	09:20	12.8	60
Control 2	55 47.04N, 004 55.53W	03/06/2010	11:05	15	60
Control 2	55 44.87N, 004 54.42W	03/06/2010	13:45	15	60
Control 2	55 45.58N, 004 53.34W	03/06/2010	15:38	15	60
Control 2	55 45.58N, 004 53.36W	04/06/2010	09:40	13.4	60
NTZ	55 31.73N, 005 41.30W	28/06/2010	12:53	15.4	60
Control 1	55 32.23N, 005 06.77W	28/06/2010	13:04	16.7	60
NTZ	55 32.29N, 005 06.30W	28/06/2010	14:12	18.5	60
NTZ	55 32.74N, 005 05.39W	28/06/2010	14:32	16.8	60
Control 1	55 32.45N, 005 04.23W	28/06/2010	15:50	16	60
Control 1	55 31.79N, 005 07.43W	28/06/2010	16:06	15	60
NTZ	55 32.14N, 005 05.55W	29/06/2010	08:22	16	60
NTZ	55 32.53N, 005 05.85W	29/06/2010	08:49	15.5	60
Control 1	55 31.36N, 005 05.01W	29/06/2010	09:35	15	60
Control 1	55 30.85N, 005 04.41W	29/06/2010	10:11	14.5	60
Control 1	55 30.70N, 005 04.93W	29/06/2010	10:49	15.9	60
Control 1	55 31.79N, 005 07.43W	29/06/2010	11:30	18.5	60
Control 1	55 31.28N, 005 06.54W	29/06/2010	12:41	16	60
NTZ	55 32.61N, 005 04.98W	29/06/2010	13:01	17.1	60
Control 1	55 31.48N, 005 03.76W	29/06/2010	14:07	16.4	60
Control 1	55 32.28N, 005 06.39W	29/06/2010	14:35	15.9	60

2.4.2.3. *Image and Data Analysis*

Images were viewed and edited in Adobe Photoshop CS6[®] to enhance the contrast and lighting to enable the species and number of individual fish and crustaceans in each image to be recorded. For each species, the abundance indices the maximum number of individuals seen in a single image (Max_N), the time taken for the first individual to arrive ($t_{arrival}$) and time to reach Max_N (t_{MaxN}) were recorded in each deployment. Max_N is a commonly used measure of relative abundance (Priede et al. 1994, Watson et al. 2009) and prevents individual fish being repeatedly recorded and provides a conservative estimation of the number of fish seen in a BUC drop (Harvey et al. 2007a, Langlois et al. 2010). $t_{arrival}$ may relate to fish abundance, based on the principle that if abundance is high, a randomly dropped camera is likely to land close to a fish, and therefore it will quickly arrive in the field of view. Where fish are more sparsely distributed it should, on average, take longer for the first fish to arrive (Priede et al. 1990, Priede et al. 1994). t_{MaxN} is also related to abundance as the higher the number of fish in a deployment area the quicker the arrival of individuals will reach Max_N and has been recorded in a number of other BUC studies (Willis and Babcock 2000, Stoner et al. 2008).

The following statistical tests were used to test the hypothesis of objective that the BUC system would be able to gather data on the diversity and relative abundance of fish and crustacean between sites. The response variable Max_N for total crustacean and fish species and the predictor variable “site” was modelled using a Generalized Linear Model (GLM). GLMs are particularly useful for modelling count data. Count data can often have a variance greater than the mean, known as overdispersion. Overdispersion was explored in the response variable Max_N by calculating the ratio between the mean and the variance. If overdispersion was detected a GLM with a negative binomial distribution was used using the statistical programme R and the package pscl, which represent models appropriate for the modelling of overdispersed data. Diagnostic plots from the models, including the distribution of the model residuals and the normal scores of standardised residual deviance were examined.

$t_{arrival}$ and t_{MaxN} are measures of the time to the occurrence of an event, crustacean or fish arrival and number reaching Max_N during the deployment. Where there were no arrivals within the observation period, this was known as censored data. This was taken into

account using a sensitivity analysis commonly used to examine and model the time to an event; usually death in biomedical research (Klein and Moeschberger 2003) but can also be applied to other censored data, such as that generated by BUC studies. t_{arrival} and t_{maxN} data can also be described as censored time to event data as the event of interest (arrival or Max_N) may occur only after the deployment. The methods used in the Cox Proportional Hazard (CPH) model, by Cox (1972), to examine the effect of covariates on survival data distribution, are designed to deal with right censored data. The relationship between the t_{arrival} and t_{maxN} of crustaceans and fish in the BUC field of view and the explanatory variable site was therefore modelled using a CPH model using a survival analysis in the statistical package survival in R. The hazard function is central to survival analysis and refers to the probability that the event of interest occurs in the interval. The primary assumption of the CPH model is of proportional hazards, meaning that the hazard ratio for two groups remains constant with time. For example, if the chance of the event for one group is twice that of another, this remains constant (Bewick et al. 2004). This assumption was tested for each covariate using the `cox.zph` test function also in the R survival package, which involves correlating the corresponding set of scaled Schoenfeld residuals with the Kaplan-Meier estimate of the survival function. Graphs of the scaled residuals against time transformed by the Kaplan-Meier estimation were plotted to check that there was no systematic departure from the horizontal line which would indicate non-proportionality.

The effect of site on fish and crustacean assemblages based on the Max_N , t_{arrival} and t_{maxN} was analysed using the multivariate statistics package PRIMER ver. 6.0 (Version 6. Primer-e, UK). Initially replicated data of the three abundance metrics were $\log(x + 1)$ transformed to down-weight the importance of the highly abundant species. The species richness of the crustacean and fish assemblages recorded by each deployment was calculated however, as many deployments contained a single crustacean or fish species, or none, other diversity indices were not calculated as they would provide little useful information on the assemblage diversity. The effect of site on crustacean and fish species richness was analysed using a GLM. Differences in assemblage Max_N , t_{arrival} and t_{maxN} were examined between sites and visualised in non-metric multi dimensional scaling (nMDS) plots and explored using a one-way crossed ANOSIM using the Bray-Curtis coefficient of similarity. A SIMPER analysis examined the role of individual species in the average Bray-Curtis dissimilarity based on the three indices of abundance

analysed. SIMPER analysis was only conducted on abundance indices for which the ANOSIM analysis found site had a significant effect.

2.5. **Results**

2.5.1. Objective 1

2.5.1.1. *Camera Settings*

From the series of camera settings test deployments the videos were of poor quality and could not enable accurate species identifications to be made. The settings in Table 2.2 and the equipment configuration in Fig. 2.1 produced the best quality stills images. The chosen configuration was developed to minimise backscatter and the length of the light path between the strobes.

Table 2.2. Sealife DC 800/1000 digital camera settings used in baited underwater camera deployments in the Firth of Clyde, West coast Scotland.

<u>Mode</u>	<u>Setting</u>
Scene Mode	Extflash
Size	3264 x 2448
Quality	Superfine
Sharpness	Hard
White Balance	Extflash Auto
ISO	Auto
Metering	Centre
Focus	Infinity
Flash	Infinity

2.5.1.1. *Lighting Effects*

When lights flashed individual fish from the species (*P. virens*, *C. rupestris* and *S. canicula*) remained at their original position at the bait.

2.5.1.2. Species Attracted and Duration of BUC Deployments

Six crustacean species (*Cancer pagurus*, *Carcinus maenas*, *Liocarcinus depurator*, *Munida rugosa*, *Necora puber* and *Pagurus bernhardus*) and 10 fish species (*Ctenolabrus rupestris*, *Gadus morhua*, *Labrus bergylta*, *Molva molva*, *Pleuronectes platessa*, *Pollachius virens*, *Raja clavata*, *Scyliorhinus canicula*, *Thorogobius ephippiatus* and *Trisopterus minutus*) were recorded at the BUC in the five test deployments.

In each of the five deployments all fish and crustacean species arrived in the first 60 minutes. The number of species in the subsequent two hours declined with deployment time (Table 2.3 a – e). The Max_N of crustacean and fish species in the five deployments occurred between 1050 and 2490 seconds and ranged between 3 and 9 individuals recorded at once (Fig. 2.3).

Table 2.3. a - e. Tables of crustacean and fish species attracted every hour to three hour long baited underwater camera deployments from Keppel Pier, Isle of Cumbrae, West coast Scotland.

a)

Species		
0 – 3600 seconds	3630 - 7200 seconds	7230 – 10800 seconds
<i>Cancer pagurus</i> <i>Carcinus maenas</i> <i>Gadus morhua</i> <i>Liocarcinus depurator</i> <i>Pagurus bernhardus</i> <i>Molva molva</i> <i>Raja clavata</i> <i>Trisopterus minutus</i>	<i>Cancer pagurus</i> <i>Carcinus maenas</i> <i>Gadus morhua</i> <i>Liocarcinus depurator</i>	<i>Carcinus maenas</i> <i>Liocarcinus depurator</i>

b)

Species		
0 – 3600 seconds	3630 - 7200 seconds	7230 – 10800 seconds
<i>Liocarcinus depurator</i> <i>Necora puber</i> <i>Pleuronectes platessa</i> <i>Scylliorhinus canicula</i>	<i>Necora puber</i> <i>Scylliorhinus canicula</i>	<i>Liocarcinus depurator</i>

c)

Species		
0 – 3600 seconds	3630 - 7200 seconds	7230 – 10800 seconds
<i>Cancer pagurus</i> <i>Carcinus maenas</i> <i>Ctenolabrus rupestris</i> <i>Necora puber</i> <i>Gadus morhua</i> <i>Liocarcinus depurator</i> <i>Pollachius virens.</i> <i>Thorogobius ephippiatus</i>	<i>Thorogobius ephippiatus</i>	<i>Necora puber</i>

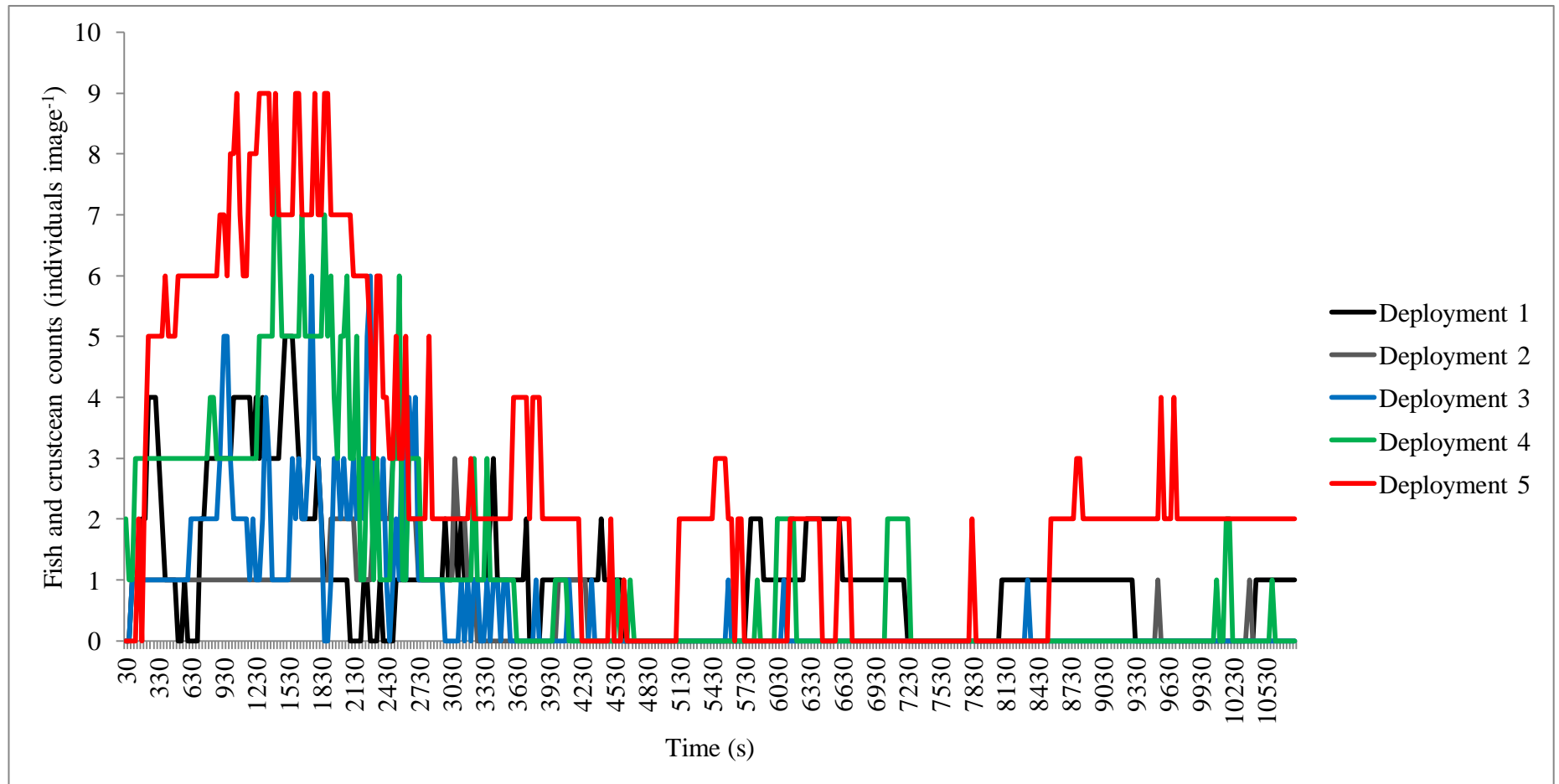
d)

Species		
0 – 3600 seconds	3630 - 7200 seconds	7230 – 10800 seconds
<i>Carcinus maenas</i> <i>Munida rugosa</i> <i>Necora puber</i> <i>Pagurus bernhardus</i> <i>Pomatoschistus microps</i> <i>Scyllorhinus canicula</i>	<i>Necora puber</i> <i>Pagurus bernhardus</i> <i>Pomatoschistus microps</i> <i>Scyllorhinus canicula</i>	<i>Necora puber</i> <i>Scyllorhinus canicula</i>

e)

Species		
0 – 3600 seconds	3630 - 7200 seconds	7230 – 10800 seconds
<i>Cancer pagurus</i> <i>Carcinus maenas</i> <i>Ctenolabrus rupestris</i> <i>Labrus bergylta</i> <i>Necora puber</i>	<i>Cancer pagurus</i> <i>Necora puber</i>	<i>Cancer pagurus</i> <i>Necora puber</i>

Figure 2.3. Plot of the arrival pattern of crustaceans and fish species at five test baited underwater camera deployments from Keppel Pier, Isle of Cumbrae, West coast Scotland.



2.5.2. Lamlash Bay Results

2.5.2.1. *Species Richness*

7 crustacean and 10 fish species were observed overall at the NTZ and the two control sites. *Liocarcinus depurator*, *Carcinus maenas* and *Pagurus bernhardus* were common across all sites. The squat lobster (*Munida rugosa*) was only found in Control 1 and *Hya areneus* only at Control 2. *Pomatoschistus microps* and *Scyllorhinus canicula* were common to all sites. *Melanogrammus aeglefinus* and *Pleuronectes platessa* were only observed at Control 1 and *Blennius ocellaris*, *Ctenolabrus rupestris*, *Gobiusculus flavescens*, *Molva molva* and *Thorogobius ephippiatus* were only at Control 2 (Table 2.4).

The mean (\pm SE) species richness of crustaceans recorded in BUC deployments was highest in the NTZ (2.17 species \pm 0.16 deployment⁻¹) and lowest in Control 1 (1.63 species \pm 0.15). A mean 1.75 species \pm 0.25 deployment⁻¹ were recorded in deployments in Control 2. The species richness of fish was however, highest in deployments in both control sites; Control 1 (1.25 species \pm 0.14 deployment⁻¹) and Control 2 (1.25 species \pm 0.18), compared to in deployments in the NTZ (0.83 species \pm 0.16). The species richness of crustaceans or fish did not vary significantly between sites (t-value = -0.170, $P > 0.05$ and t-value = 0.000, $P < 0.05$).

Table 2.4. Fish and crustacean species observed in baited underwater camera deployments in Lamlash Bay no-take zone (NTZ) and two control sites.

NTZ	Control 1	Control 2
<i>Cancer pagurus</i>	<i>Carcinus maenas</i>	<i>Hya araneus</i>
<i>Carcinus maenas</i>	<i>Liocarcinus depurator</i>	<i>Blennius ocellaris</i>
<i>Liocarcinus depurator</i>	<i>Melanogrammus aeglefinus</i>	<i>Cancer pagurus</i>
<i>Necora puber</i>	<i>Munida rugosa</i>	<i>Carcinus maenas</i>
<i>Pagurus bernhardus</i>	<i>Necora puber</i>	<i>Ctenolabrus rupestris</i>
<i>Pomatoschistus microps</i>	<i>Pagurus bernhardus</i>	<i>Gobiusculus flavescens</i>
<i>Scyliorhinus canicula</i>	<i>Pomatoschistus microps</i>	<i>Liocarcinus depurator</i>
<i>Trisopterus minutus</i>	<i>Pleuronectes platessa</i>	<i>Molva molva</i>
	<i>Scyliorhinus canicula</i>	<i>Pagurus bernhardus</i>
		<i>Pomatoschistus microps</i>
		<i>Scyliorhinus canicula</i>
		<i>Trisopterus minutus</i>
		<i>Thorogobius ephippiatus</i>

2.5.2.2. Max_N

The mean crustacean Max_N per deployment was highest in the NTZ (4.33 individuals \pm 0.39 deployment⁻¹) and lowest in Control 2 (1.88 \pm 0.29). In Control 1 a mean 2.13 individuals \pm 0.35 deployment⁻¹ were observed. The mean Max_N of fish observed in BUC deployments was highest in Control 1 (1.63 individuals \pm 0.16 deployment⁻¹) and lowest in the NTZ (0.83 \pm 0.16 ⁻¹). At Control 2 1.5 individuals \pm 0.3 deployment⁻¹ were observed (Fig. 2.4). The Max_N for crustaceans and fish species were over dispersed therefore a Generalized Linear Model with a negative binomial distribution was used to analyse both data sets. GLM analysis revealed that there was a significant difference between the Max_N for crustacean species at the three sites (z-value = -1.989, $P < 0.05$).

GLM analysis found no significant difference between the Max_N for fish species at the three sites ($z\text{-value} = 0.766$, $P = 0.444$).

2.5.2.3. t_{arrival}

On average (\pm SE) the first crustaceans arrived fastest in NTZ deployments (405 ± 120.19 seconds) and slowest in Control 2 (2028 ± 156.98 seconds). The first crustacean arrived on average after 1043 ± 198.65 seconds at deployments in Control 1. The first fish arrived at Control 1 on average the fastest, after 1226 ± 153.3 seconds, and longest at the NTZ (2255 ± 375.8 seconds). It took an average 1946 ± 223 seconds for the first fish to arrive in deployments in Control 2 (Fig. 2.5). Survival analysis revealed that there was a significant difference between the t_{arrival} of crustaceans between the three sites ($z = -2.077$, $P < 0.05$). The t_{arrival} of fish species were not significantly different between the three sites ($z\text{-value} = 0.36$, $P = 0.719$).

2.5.2.4. t_{maxN}

The time to reach crustacean Max_N (t_{maxN}) was on average (\pm SE) shortest in NTZ (870 ± 188.52 seconds) and longest in Control 2 (2028 ± 253.59 seconds). In Control 1 it took on average 2028 ± 253.59 seconds to reach the Max_N for crustaceans. The t_{maxN} was on average shortest in deployments in Control 1 (1500 ± 187.5 seconds) for fish species and took longest in the NTZ (2565 ± 427.5 seconds). In Control 2 it took on average 1644 ± 205.51 seconds for fish numbers to reach Max_N (Fig. 2.6). Survival analysis revealed that the t_{maxN} of crustacean species was significantly different between the three sites ($z\text{-value} = -2.467$, $P < 0.05$). The t_{maxN} of fish species were not significantly different between the three sites ($z\text{-value} = 0.395$, $P = 0.693$).

Figure 2.4. Mean (\pm SE) maximum number of individuals (Max_N) of crustaceans and fish species at a baited underwater camera system in Lamlash Bay no-take zone (NTZ) and two control sites.

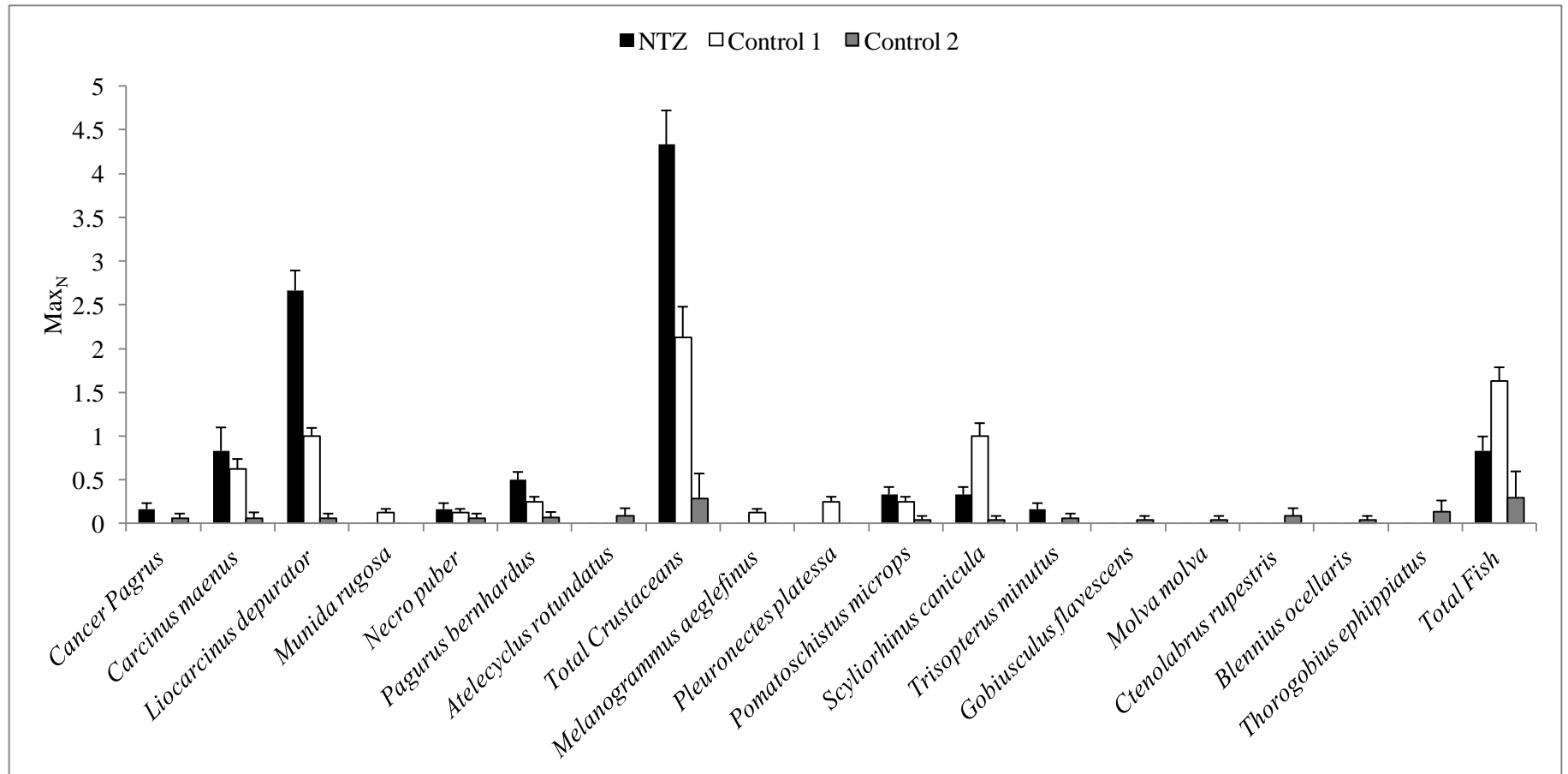


Figure 2.5. Mean (\pm SE) time to first arrival (t_{arrival}) of crustaceans and fish species at a baited underwater camera system in Lamlash Bay no-take zone (NTZ) and two control sites.

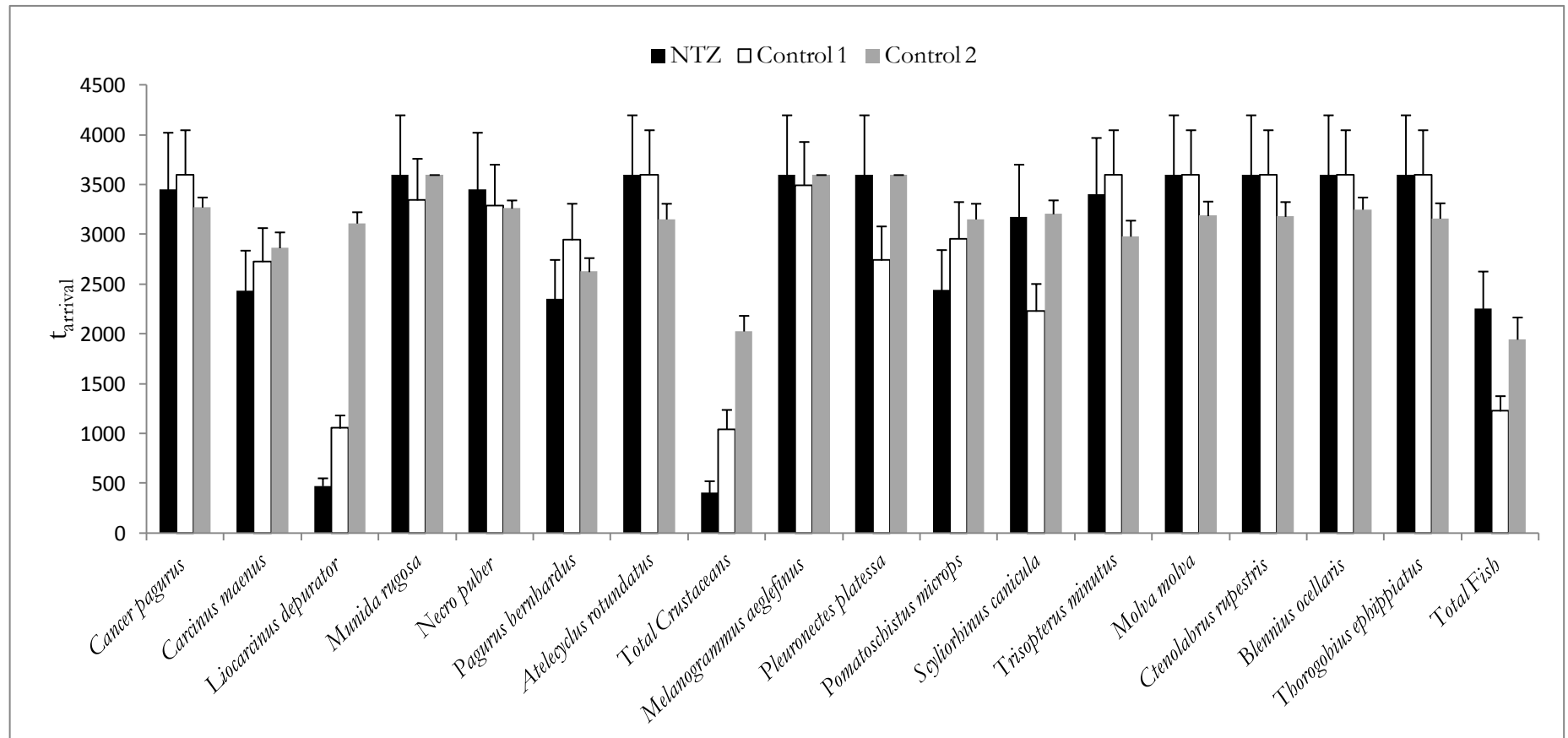
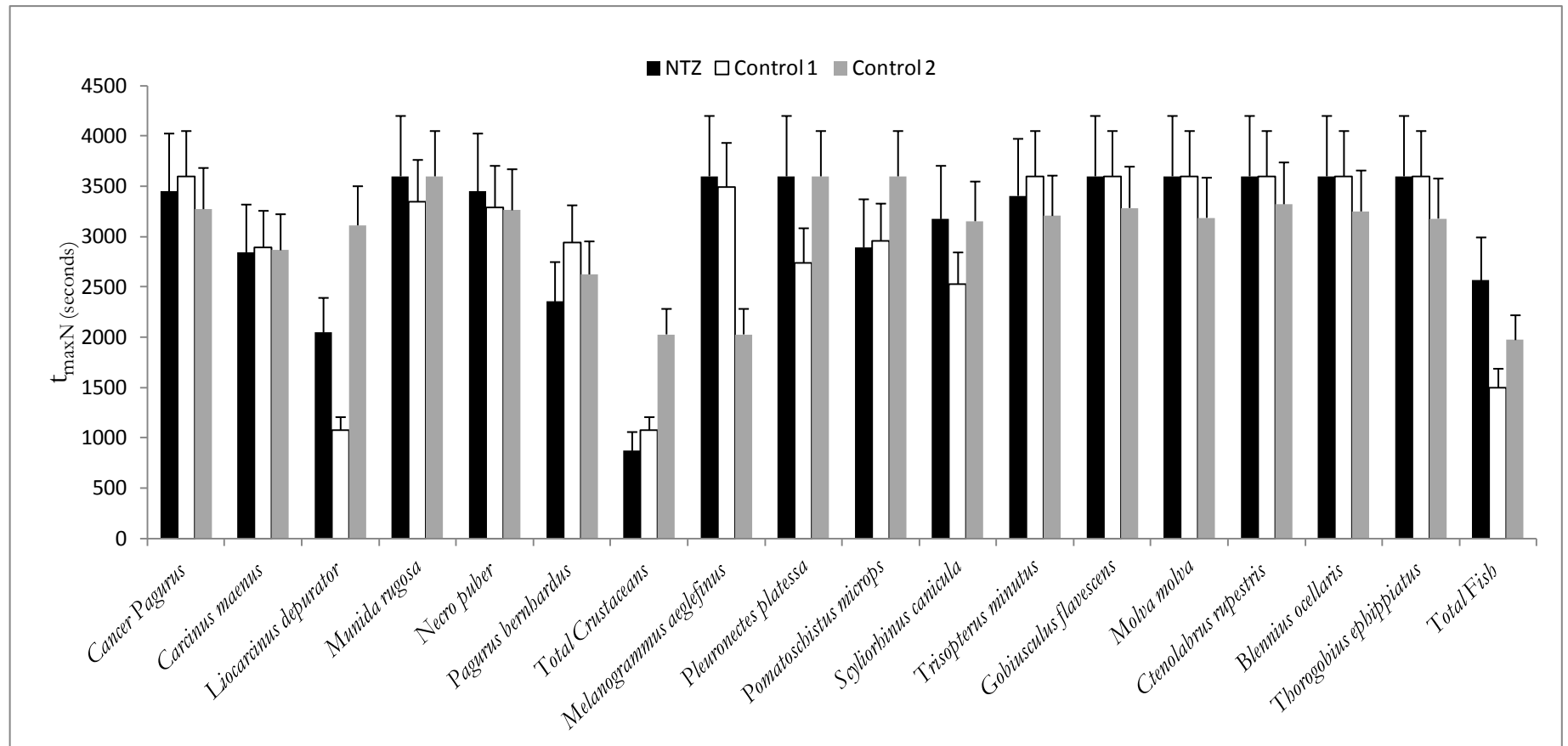


Figure 2.6. Mean (\pm SE) time to reach Max_N ($t_{\text{max}N}$) of crustaceans and fish species at a baited underwater camera system in Lamlash Bay no-take zone (NTZ) and two control sites.



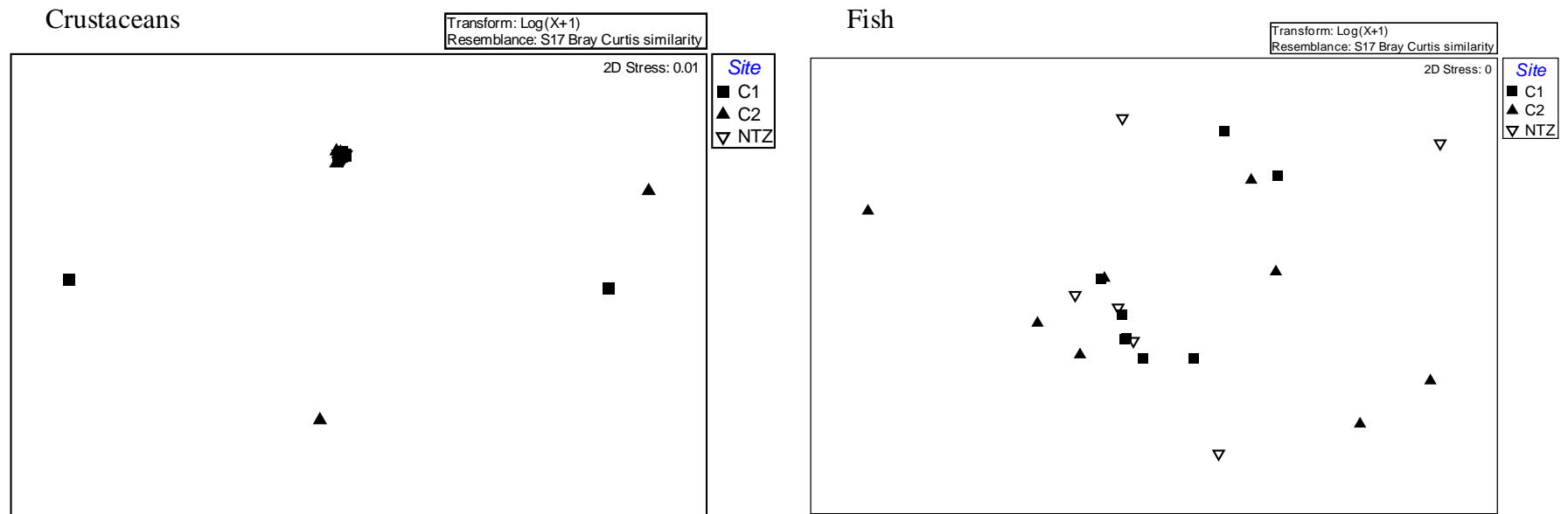
2.5.2.5. Assemblage

The crustacean and fish assemblages observed by the BUC system at the three sites were compared using multi-dimensional scaling plots and ANOSIM and SIMPER analysis. There was no significant difference between the crustacean assemblages recorded at the three sites when Max_N (ANOSIM, $R = 0.07$, $P = 0.13$) was used as an index of abundance. This was also illustrated in the MDS plots which do not show any patterns of clustering of data collected at individual sites (Fig. 2.7 a - c). However, when t_{arrival} (ANOSIM, $R = 0.15$, $P = 0.01$) and t_{maxN} ($R = 0.177$, $P = 0.005$) were used as an index of crustacean abundance a weak separation between the assemblages observed at the three sites was observed. Pairwise comparison tests showed that significant differences in crustacean assemblages, for both time based abundance metrics (t_{arrival} and t_{maxN}), existed between Control 2 and the other two sites. The t_{arrival} of *L. depurator*, *P. bernhardus* and *C. maenas* was lower in Control 2 and responsible for > 85 % of the difference in the assemblage observed between the NTZ and Control 2 in the SIMPER analysis. The t_{arrival} of *L. depurator* and *C. maenas* was lower in Control 2 compared to Control 1 but lower for *H. araneus* in Control 1. These three species were responsible for > 80 % of the difference in crustacean assemblages between Control 1 and 2 (Table 2.6). The t_{maxN} of *C. maenas*, *P. bernhardus* and *L. depurator* were higher in the NTZ and *N. puber* was the only species with a lower t_{maxN} in the NTZ. These four species were responsible for > 80 % of the difference in the crustacean assemblages between Control 2 and the NTZ. The same four species were responsible for > 85 % of the difference between Control 1 and 2. The average abundances of *L. depurator* and *N. puber* were lower in Control 2 and *C. maenas* and *P. bernhardus* average abundances were lower in Control 1 (Table 2.7).

The ANOSIM analysis found no significant difference between the fish assemblages recorded at the three site when either Max_N (ANOSIM, $R = 0.01$, $P = 0.36$), t_{arrival} (ANOSIM, $R = 0.01$, $P = 0.38$) and t_{maxN} (ANOSIM, $R = -0.04$, $P = 0.82$) were used as indices of abundance. MDS plots (Fig. 2.7 a - c) do not show any patterns of clustering of data collected at individual sites.

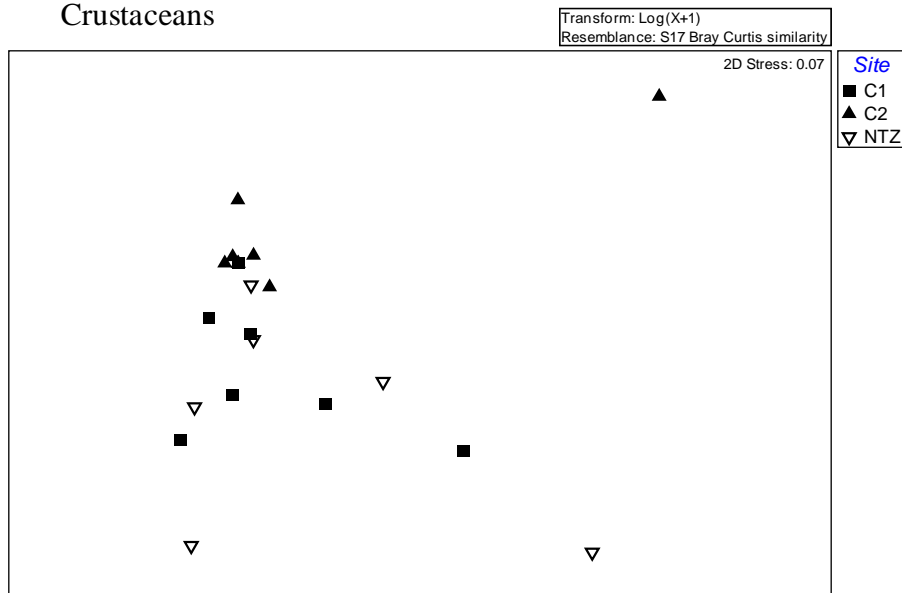
Figure 2.7. a – c. Bray-Curtis similarity and Multi-Dimensional Scaling (MDS) analysis to compare the abundance indices a) the mean maximum number of individuals (Max_N) b) the first arrival time (t_{arrival}) and c) the time to reach Max_N (t_{max_N}) of crustacean and fish assemblages between Control 1 (C1), Control 2 (C2) and the no-take zone (NTZ).

a)

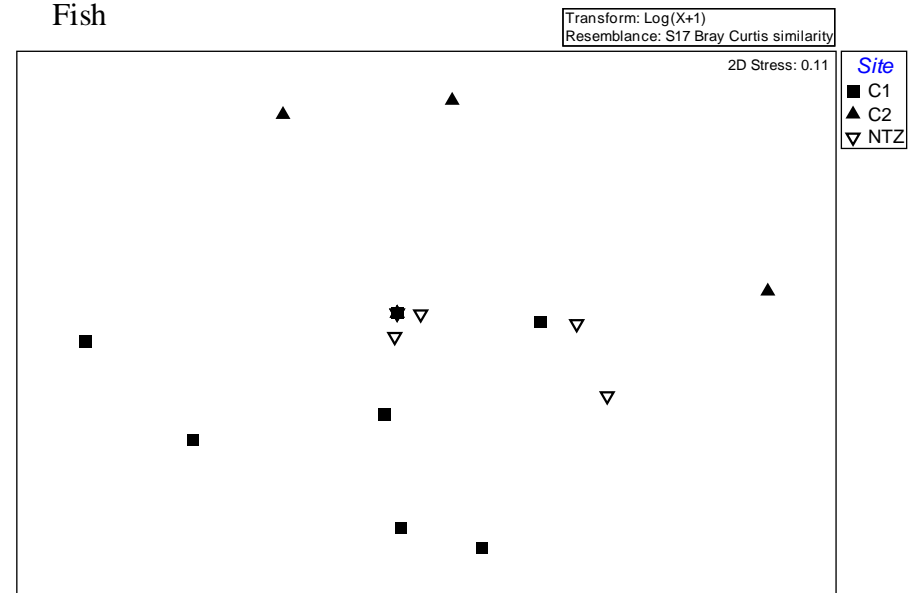


b)

Crustaceans

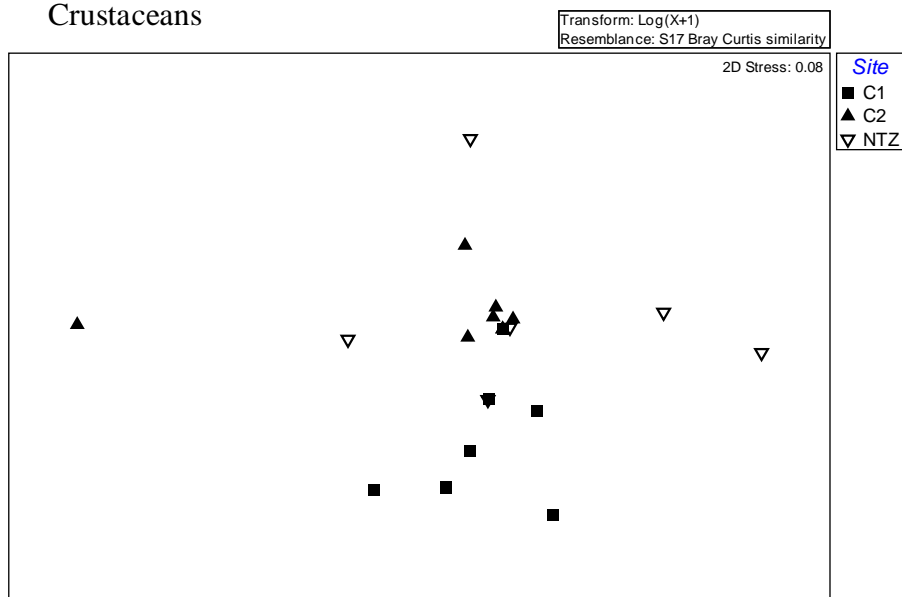


Fish



c)

Crustaceans



Fish

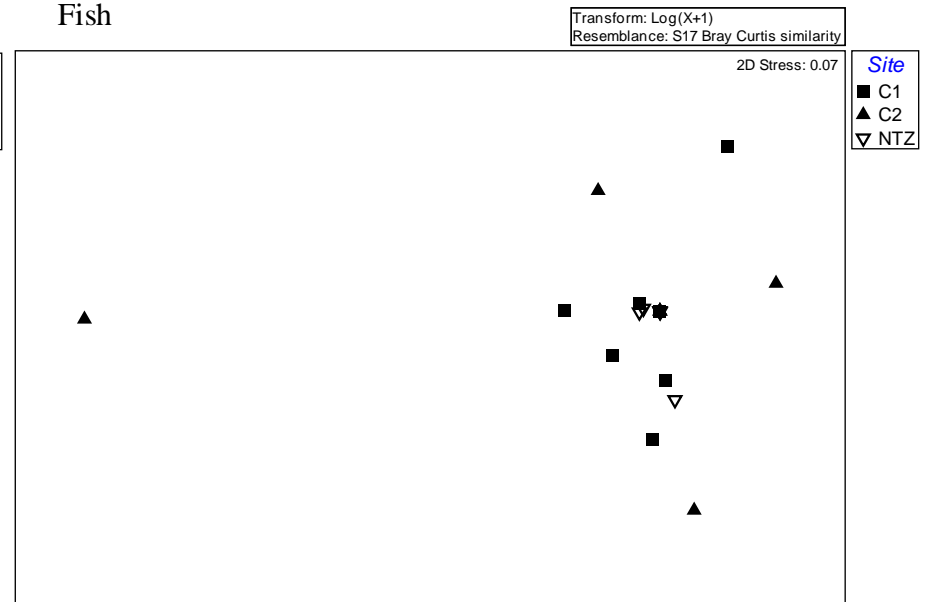


Table 2.5. Species, ranked in order of importance, contributing to the average dissimilarities between scavenger assemblages recorded in baited underwater camera deployments in a) Control 1 (C1) and Control 2 (C2) and b) Control 2 and Lamlash Bay no-take zone (NTZ) as determined by similarity percentages (SIMPER) analysis based on the time to first arrival (t_{arrival}) of crustaceans at the baited underwater camera.

a) Control 1 (C1), Control 2 (C2)

Average Dissimilarity = 5.00

Species	Av.abund (C1)	Av.abund (C2)	Av.Diss	Diss/SD	Contri%	Cumm%
<i>Liocarcinus depurator</i>	5.71	7.99	2.23	1.51	44.49	44.49
<i>Carcinus maenas</i>	7.36	7.50	1.21	0.67	24.24	68.74
<i>Hya araenas</i>	8.19	7.59	0.60	0.37	11.96	80.70
<i>Pagurus bernhardus</i>	7.86	7.77	0.52	1.02	10.34	91.04

b) NTZ, Control 2 (C2)

Average Dissimilarity = 6.64

Species	Av.abund (NTZ)	Av.abund (C2)	Av.Diss	Diss/SD	Contri%	Cumm%
<i>Liocarcinus depurator</i>	5.24	7.99	2.61	1.85	39.31	39.31
<i>Pagurus bernhardus</i>	6.70	7.77	1.57	0.89	23.56	62.87
<i>Carcinus maenas</i>	6.90	7.50	1.55	0.80	23.36	86.23
<i>Hya araenas</i>	8.19	7.59	0.61	0.37	9.19	95.46

Table 2.6. Species, ranked in order of importance, contributing to the average dissimilarities between scavenger assemblages recorded in baited underwater camera deployments in a) Control 1 (C1) and Control 2 (C2) and b) Control 2 and Lamlash Bay no-take zone (NTZ) as determined by similarity percentages (SIMPER) analysis based on the time to Max_N (t_{maxN}) of crustaceans at the baited underwater camera.

a) Control 1 (C1), Control 2 (C2)

Average Dissimilarity = 5.32

Species	Av.abund (C1)	Av.abund (C2)	Av.Diss	Diss/SD	Contri%	Cumm%
<i>Liocarcinus depurator</i>	5.90	7.99	2.03	1.51	44.68	44.68
<i>Carcinus maenas</i>	7.81	7.50	0.89	0.61	19.61	64.29
<i>Hya araneas</i>	8.19	7.59	0.59	0.37	13.08	77.36
<i>Pagurus bernhardus</i>	8.00	7.77	0.43	1.00	9.44	86.80

b) NTZ, Control 1 (C1)

Average Dissimilarity = 6.64

Species	Av.abund (NTZ)	Av.abund (C1)	Av.Diss	Diss/SD	Contri%	Cumm%
<i>Liocarcinus depurator</i>	7.46	5.90	1.83	1.63	34.33	34.33
<i>Necor puber</i>	6.78	7.85	1.41	0.88	26.55	60.88
<i>Pagurus bernhardus</i>	7.38	8.00	0.87	0.55	16.42	77.30
<i>Carcinus maenas</i>	7.63	7.81	0.73	0.73	13.73	91.03

2.6. Discussion

2.6.1. Objective 1

From the series of test deployments a number of important observations were made that enabled an effective BUC configuration and deployment procedure for the West coast of Scotland waters to be found. The system attracted a range of predatory and scavenging crustacean and fish species. The stills images produced when the camera was in time-lapse mode enabled accurate species identification, which video did not. Strobe lighting did not affect the feeding behaviour of crustacean and fish commonly observed at the bait of the BUC system. In all five three hour long test deployments all crustacean and fish species arrived within approximately the first hour of the deployment and it was within this hour the arrival and Max_N of each species was observed.

From these observations it was therefore concluded that the underwater camera would be set in time lapse mode with the camera setting, described in Table 2.2, and in the frame position found to produce the best images (Fig. 2.1) Strobe lighting was necessary as poor visibility was often experienced and would be used to illuminate the camera field of view. Mackerel bait was able to attract a range of crustacean and fish species and is readily available all over Scotland either wild caught or purchased. From the results of the test deployments it was concluded that hour long BUC deployments were the most appropriate in ensuring that all species attracted to the BUC were recorded and including in subsequent analysis. This time period was also appropriate for recording the Max_N of the predatory and scavenging assemblages observed and would enable t_{arrival} , t_{maxN} and Max_N to be used as an indices of relative abundance. The BUC methodology described in the chapter was used in the Scottish Industry Science Partnership project “Development and evaluation of methods for surveying fish population s in nearshore waters”. The method was used to make relative comparisons of the fish assemblages in the Firth of Clyde, Sound of Mull, Sound of Kerrera, Mull of Galloway and Loch Sunart (Smith et al. 2010).

The fish and crustacean species observed in these BUC deployments are all common species within the Clyde Sea Area and have been commonly observed in *Nephrops* trawls (Bergmann et al. 2002, Stratoudakis et al. 2001). Nickell and Moore’s 1992 two

BUC deployments in the Firth of Clyde also attracted some of the same crustacean species (*C. pagurus*, *L. depurator*, *P. bernhardus* and *H. araneus*) as the current study. However, it is difficult to make comparison with these results as the camera system in the previous study was reported to leave the seabed for substantial periods of time (> 1 hour). Frozen cod fillet, contained inside a funnel trap placed on the sea bed, was used as bait however, the amount is not reported. Even though, in the first study similar first arrival times (8 minutes) of *L. depurator* were reported but longer arrival times were found for *P. bernhardus* (35 minutes). There was no report of fish species being attracted to the BUC. Howarth et al. (2012) BUC deployments in Lamlash Bay in 2011 recorded some of the same species as this study; *N. puber*, *G. morhua*, *Pagurus* spp., *L. depurator*, *M. rugosa*, *S. canicula* and unspecified wrasse and goby species. Video was used in these deployments which may have made species identification more difficult than in the stills images. These deployments were also one hour long and used 200 g of mackerel bait making them comparable to the BUC deployments described in this study however, the camera was positioned slightly lower on the seabed. Howarth's study however, recorded relatively high number of whiting (*Merlangius merlangus*) and haddock (*Melanogrammus aeglefinus*) which were not observed in the present study.

During the development of a baited underwater video study in the Cape Rodney to Okakari Point (CROP) Marine Reserve, New Zealand three test deployments were made to determine the BUC duration within which pink snapper (*Pagurus auratus*) and blue cod (*Parapercis colias*) Max_N was recorded. 70 % of the snapper observed in the 60 minute deployment were observed in the first 30 minutes and for both species Max_N occurred within the first 30 minutes (Willis and Babcock 2000). High densities of *P. auratus* and *P. colias* are found within the CROP marine reserve which would explain the quick accumulation of individuals at the BUC (Taylor et al. 2005). 30 minute long baited underwater video deployments have been used since 2000 and now form an integral role in the CROP reserve monitoring programme (Taylor et al. 2005, Sivaguru 2008). One hour long deployments of the baited remote underwater video system are used to study the relative abundance of fish fauna of reefs and MPAs in Western Australia (Harvey et al. 2007, Watson et al. 2005).

2.6.2. Objective 2

GLM analysis found that the abundance indices (Max_N , t_{arrival} and t_{maxN}) indicated that the total crustacean abundance was highest in the NTZ and lowest in Control 2. GLM analysis found no significant differences between any of three abundance indices derived from the arrival pattern of fish at the BUC system. The fish and crustacean assemblages observed in the BUC systems between the three sites (Lamlash Bay NTZ and the two control sites) showed relative little difference when the abundance indices; Max_N , t_{arrival} and t_{maxN} , were used. When t_{arrival} and t_{maxN} were used as indices a difference was observed between the crustacean assemblages in Control 2 and the NTZ and Control 1. This was mainly the result of an individual from the three most crustacean species (*C.maenas*, *P. bernhardus* and *L. depurator*) taking longer to arrive at the BUC in Control 2 and also for the number of individuals of that species to reach Max_N .

These results indicate that at the time of study the scavenger/carnivorous crustacean and fish assemblages observed between the NTZ and the two control sites were relatively similar. Control sites do have similar habitats to the NTZ which is likely to result in similar assemblages developing. The Firth of Clyde has been described as a highly degraded marine ecosystem from the effects of overfishing and suggests that communities will only be able to recover if the pressures of bottom trawling are removed (Thurstan and Roberts 2010). Conservation measures such as the Lamlash Bay NTZ aim to enable marine communities to recover free of exploitation pressures however, the onset of recovery inside the NTZ can be considerable, especially for predatory fish species (Russ and Alcala 2004). However, few long term studies exist of the impact of NTZs making it difficult to determine the time required for recovery (Russ and Alcala 2004). The Firth of Clyde has been described as an ecosystem almost overfished to the point where nothing worth catching remains and that irreversible damage to the biodiversity and productivity of the ecosystems (Thurstan and Roberts 2010). This would indicate that the onset of recovery of the protected communities within this ecosystem would be predicted to take longer than in other less degraded ecosystems and it would be surprising if a recover within the NTZ was recorded after two years establishment. However, Heath and Speirs (2012) examined changes in the biomass density, species diversity and length structure of demersal fish communities in the Firth of Clyde from trawl surveys between 1927 and 2009. There was a decline in the number of large fish (< 40 cm) caught within the Clyde and the evenness of the species

composition was lower than observed in neighbouring areas but a limited impact on species richness was observed. However, an increase in the biomass density of small demersal fish (< 40 cm) was observed. The results may indicate that demersal fish communities in the Firth of Clyde may have the potential for recovery within the NTZ.

The absence of comparable data from before the NTZ hampers interpretation of this finding. Even though, the three indices (Max_N , t_{arrival} and t_{maxN}) indicate that total crustacean abundance is higher at the time of the study it is impossible to attribute this to the effect of NTZ protection. The study would need to be repeated to determine the temporal variation in crustacean abundances. The data collected in this study would be most suitable to serve as a baseline BUC data against which further studies' results could be compared, such as that by Howarth et al. (2012). With sufficient temporal replication to encompass the temporal fluctuations in population such studies could enable an analysis on the impact of the NTZ on predatory and scavenging crustacean and fish communities. BUCs are cost-and-time efficient means to collect data on these communities which would enable data to be collected frequently at a low cost and effort.

Howarth et al's (2012) baited camera study concluded that the area, regardless of protection status still only supports low diversity communities dominated by scavenging invertebrates, such as crustaceans and starfish. However, unlike the present study Howarth et al (2012) found that the mean abundance of crustaceans was higher in the open area that corresponded to Control 1. The 2011 BUC surveys undertaken by Howarth et al. (2012) recorded significantly higher numbers of juvenile gadoids dominated by whiting (*Merlangius merlangus*), haddock (*Melanogrammus aeglefinus*) and cod (*Gadus morhua*), within the NTZ. However, these species were not observed in the NTZ or adjacent open areas during the present study even though deployments using this system in other locations on the West coast of Scotland and Sweden have attracted juveniles of these species. The eggs and larvae of gadoids are transported to inshore waters on currents, with juveniles subsequently making the transition from a pelagic to demersal habit (Demain et al. 2011). A number of studies (Graham and Carruthers 1926, Bromley and Kell 1999) have reported that juvenile cod begin the transition in early June and become increasingly demersal throughout July (Bromley and Kell, 1999) and that haddock settlement occurs for approximately 1 month between June and September (Koeller et al. 1986, Demain et al. 2011). Whiting appear to have a more extended

period of settlement that begins in June and continues until the beginning of August (Hislop 1984, Demain et al. 2011). The diet of juvenile cod, haddock and whiting also shifts as they grow throughout the year becoming more reliant on fish and crustaceans (Greenstreet et al. 1999, Demain et al. 2011). It is possible that the presence of juvenile gadoids in Howarth et al's (2012) surveys during 2011, compared to their absence in our surveys in 2010 represents the beginning of recruitment into the area. However, Howarth et al's (2012) survey took place in July/August 2011 whereas our survey was in late June. Therefore it is possible that more juveniles would have become established in the demersal environment and to have developed a piscivorous diet by the time of Howarth et al's work.

The BUC methodology described in this chapter can be used to make relative comparisons of scavenging and predatory crustacean and fish assemblages between sites. However, the generation of absolute abundance estimates would enable comparison of BUC data with data collected via other survey methods, i.e. underwater visual census surveys by divers and trawl surveys. Absolute abundances would also enable changes in assemblages to be related to conservation targets. Chapter 5 describes a modelling methodology designed to generate absolute abundance estimates of temperate fish species from BUC data.

2.7. Conclusion

This work describes a BUC methodology that effectively attracts a range of predatory and scavenging fish and crustacean species in the cold temperate waters of the West coast of Scotland. The method is used to gather data on the relative differences between scavenger/predatory crustacean and fish assemblages between sites in the Firth of Clyde. This data also represents an initial baseline data set against which comparisons with the findings of future BUC studies in this area can be made. This will be particularly valuable in monitoring the impact of the Lamlash Bay NTZ on crustacean and fish assemblages.

2.8. Acknowledgements

This work was supported by the Scottish Industry-Science Partnership grant for the project “Development of methods for surveying nearshore fish populations”. We thank the crew of the RV Aora, the logistical support of the staff at the University Marine Biology Station Millport and the information provided by L. Howarth.

3. Chapter 3

Comparisons between baited underwater camera and visual census surveys of shallow coral reef fish communities in the northern Gulf of Aqaba

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3.1. Abstract

Baited underwater cameras (BUCs) are an increasingly popular means of monitoring inshore predatory fish communities. BUC have several attractive attributes as they are cheap, easy and safe to deploy, do not require specialist staff or vessels, and have a low impact on the habitat to be surveyed. Here, we compared the predatory fish assemblages recorded in BUC deployments (n = 16) and Underwater Visual Census (UVC) surveys (n = 16) at four sites in the northern Gulf of Aqaba, at depths of 5 - 20 m. BUC data were summarised using the standard abundance metric “Max_N” (the highest number of a species seen at one time). The time to first arrival of each species was also recorded. The Gulf of Aqaba supports unique coral reef fish assemblages and it is important to perform a study specific in this distinct biogeographical region to understand whether BUC surveys could be useful in this sensitive environment. BUCs recorded the same number of predatory fish species as the UVCs but with lower sampling effort. Max_N and time to first arrival did not correlate with population abundance estimates from UVCs, except in one species of the 10 surveyed. Until improved methods of interpreting BUC data are developed the deployment of BUCs could be used to assess predator species richness but is not able to indicate even relative variation in population abundance.

3.2. Introduction

The reefs around Eilat, Gulf of Aqaba, are at the northernmost extreme of coral distribution in the Indo-Pacific and support a unique fauna, and this makes them of scientific interest and conservation importance (Portman 2007, Brokovich et al. 2010). The Gulf of Aqaba is a distinct biogeographical region in the Red Sea which supports unique coral reef fish assemblages (Sheppard et al. 1992). Increasing levels of development and tourism in the Gulf, and in particular on the Sinai coast are known to have impacted on reef habitats (Hawkins and Roberts 1994, Golani and Diamant 1999). At the Gulf's northern tip the cities of Eilat and Aqaba add impacts from mariculture, ports, industry and urban infrastructure (Wilhelmsson et al. 1998). These reefs have experienced a significant loss of coral cover and associated marine diversity (Abelson and Shlesinger 2002, Loya 2004, 2007) and are considered to be in a critical condition by the UNEP/IUCN classification, meaning that they are severely damaged and in imminent danger of collapse or extermination. The reefs surrounding Eilat are some of the most degraded in the Gulf of Aqaba (Abelson and Shlesinger 2002).

In recognition of the unique and important nature of the northern Gulf of Aqaba region, artificial reefs and marine protected areas (MPAs) have been established on Eilat's coast to reduce coral deterioration and encourage the recovery of reef communities (Gundermann and Popper 1975, Golani and Diamant 1999). Diver based underwater visual censuses (UVC) have been used to monitor the impact of these measures on the Gulf of Aqaba's reef fish populations (Gundermann and Popper 1975, Golani and Diamant 1999, Abelson and Shlesinger 2002, Khalaf and Kochzius 2002, Brokovich et al. 2006, Brokovich et al. 2008).

UVC has been adopted for many reef fish surveys as it is a relatively cheap, rapid and non-destructive method of surveying marine populations, compared to tag and recapture studies (Thresher and Gunn 1986) and extractive techniques such as trawling and poisons (Sale and Douglas 1981, Bellwood and Alcala 1988, Watson and Quinn 1997, Stewart and Beukers 2000). The counts generated from UVC can provide information on the abundance, density and species composition of the fish community surveyed (Bellwood and Alcala 1988, Cappo et al. 2006, Harvey et al. 2007b, Stobart et al. 2007).

Despite the many advantages of UVC, the method does have known limitations. Some fish species are attracted to divers (particularly where fish feeding is common), while others retreat (Watson et al. 2005, Cappo et al. 2006, Langlois 2006). As a result cryptic or shy fish may be unrepresented and bolder more conspicuous species can be over-represented (Kulbicki 1998, Willis and Babcock 2000, Willis et al. 2000, Watson et al. 2005, Harvey et al. 2007b). Extensive time and effort is required to train a diver to accurately conduct an UVC and inter-observer variation can be considerable, making survey standardization difficult (Thresher and Gunn 1986, Harvey and Shortis 1995, Darwall and Dulvy 1996). Nevertheless, UVCs still represent one of the most widely used and accepted methods for monitoring fish populations (Brokovich et al. 2006). The maintenance of a consistent survey programme using UVC across the depth range of interest is a challenge, ideally requiring the regular use of the same trained personnel.

An alternative approach to monitoring reef populations is the use of underwater camera systems deployed from the surface. Like UVC, underwater cameras are non-destructive and relatively inexpensive, but offer a greater depth range (Jamieson et al. 2006) and a permanent record of the survey. Cameras can be deployed by personnel with only minimal training, with species identification and analysis taking place later. Cameras are used with and without bait, but the use of bait at the camera greatly increases the statistical power of the method and its ability to detect spatial and temporal variation in populations (Harvey et al. 2007b). As fish travel to the bait from a distance the stationary camera effectively surveys a large area (Watson et al. 2005). Bait also allows the presence of some cryptic species to be determined as it attracts them out of cover and into the field of view of the camera (Stewart and Beukers 2000). A known disadvantage of baited underwater cameras (BUCs) is that the assemblage observed is biased towards scavengers and predators (Armstrong et al. 1992, Priede et al. 1994), but as such species are often ecologically and economically important members of marine communities, BUCs have become important tools for coastal survey and monitoring (Willis and Babcock 2000, Watson et al. 2010). The number of foraging animals attracted to BUCs is influenced by the velocity and direction of near bottom currents due to their effect on bait plume dispersal (Thurston et al. 1995, Heagney et al. 2007). Existing BUC analysis methods either use assumptions developed for abyssal systems or do not consider plume dispersal dynamics at all and this

limits their ability to estimate absolute abundance and density (Heagney et al. 2007, McLean et al. 2010).

If BUCs are to become a mainstream marine science tool, it is important that we understand the advantages and limitations of this method. In particular we need to understand how the results compare to other, more established survey techniques. BUC survey results have been compared to those derived from trawl surveys. The abundance of the deep sea grenadier *Coryphaenoides (Nematonurus) armatus*, in the north-east Atlantic was estimated from the arrival time of the first individual at a BUC using the relationship: $n = 6 \times 10^8 / t_{\text{arrival}}^2$. This was found to correlate well with abundance of *C. armatus* observed in trawl surveys in approximately the same area and time (Priede and Merrett 1996), but this abundance relationship broke down when trawls on the Mid-Atlantic Ridge were compared to baited camera deployments (Bailey et al 2007). Similarly, shallow water BUC results in the Great Barrier Reef were compared to trawl surveys by Cappo et al. (2004) and found that the methods recorded significantly different fish assemblages. Trawl surveys primarily recorded small demersal species, such as flatfish, apogonids, synodontids, triglids and callionymids while the BUC mainly recorded larger mobile species such as elasmobranchs, caranigids, scombrids and eels. The non-destructive nature of BUCs often means that they are used within areas where fishing is prohibited (McLean et al. 2010, Dorman et al. 2012). In these areas it is often impossible to gather trawl data against which to compare BUC results therefore several studies have made comparisons with UVC surveys. UVC transect surveys in a marine reserve in the lagoon waters of New Caledonia surveyed a greater diversity and abundance of reef fish than BUC surveys (Langlois et al. 2006). However, the UVC was observed to mainly detect smaller fish while BUC results were dominated by large mobile species (Langlois et al. 2006). Watson et al. (2010) compared the fish assemblages recorded by an UVC transect method that employs a diver operated stereo video system and a stereo baited underwater camera at protected areas on the West Coast of Australia. The BUC system recorded a greater overall species richness and abundance, particularly of large, predatory species, such as emperor (*Lethrinus nebulosus*), grouper (*Plectropomus leopardus*) and moray eels (*Gymnothorax spp*).

The reef fish assemblages of the Gulf of Aqaba are unique and until now have been predominantly surveyed using UVC techniques. However, due to the time and cost

involved in the UVC surveys they have only been performed infrequently in the area. There is a local desire to find a survey method that will be more efficient and able to produce data on a more frequent basis, particularly in relation to the protected areas of the region. The use of the BUC method is new to the area and similar studies have been performed in other biogeographical regions (Langlois et al. 2006 and Watson et al. 2009). However, due to the unique nature of the fish assemblages in the Gulf of Aqaba it is seen as important to conduct a separate study here prior to the introduction of BUC surveys.

Large predatory coral reef fish species are targeted by fishermen in the Red Sea (Gala et al. 2002) meaning changes in the population distribution and abundance are closely linked to fishing pressures. Target predatory species are often the focus of MPA monitoring to assess the effect of reductions in fishing pressures (Russ and Alcala 2004, Willis et al. 2003). Marine top predators are also sensitive to fluctuations in lower trophic groups (Frank et al. 2005, Sergio et al. 2008) and can therefore potentially act as indicators of the health of the wider coral reef fish assemblage. Therefore the monitoring of the species diversity and abundance of predatory reef fish is important to understand the impact of the Eilat Coral Reserve MPA on reef fish assemblages.

3.3. Aims and Objectives

3.3.1. Objective 1

The objective of this study was to compare the predatory fish assemblage observed by UVC and BUCs in the complex shallow coral reef habitats of Eilat to enable us to determine whether BUC could be used as an additional survey method to UVC surveys to monitor predatory coral reef fish. UVCs recorded the abundances of predatory species and the results were compared to recordings from BUC deployments made at the same location within 10 days (n = 16 locations).

It was hypothesised that:

- 1) The BUC abundance metrics would correlate with population density estimates for predatory fish from UVCs surveys, allowing BUC data to be used as a proxy for predatory fish population abundance.

2) Even within the predatory fish species some species would only be seen in UVCs and some only at BUCs, meaning that no correlation would be possible for these species.

3.3.2. Objective 2

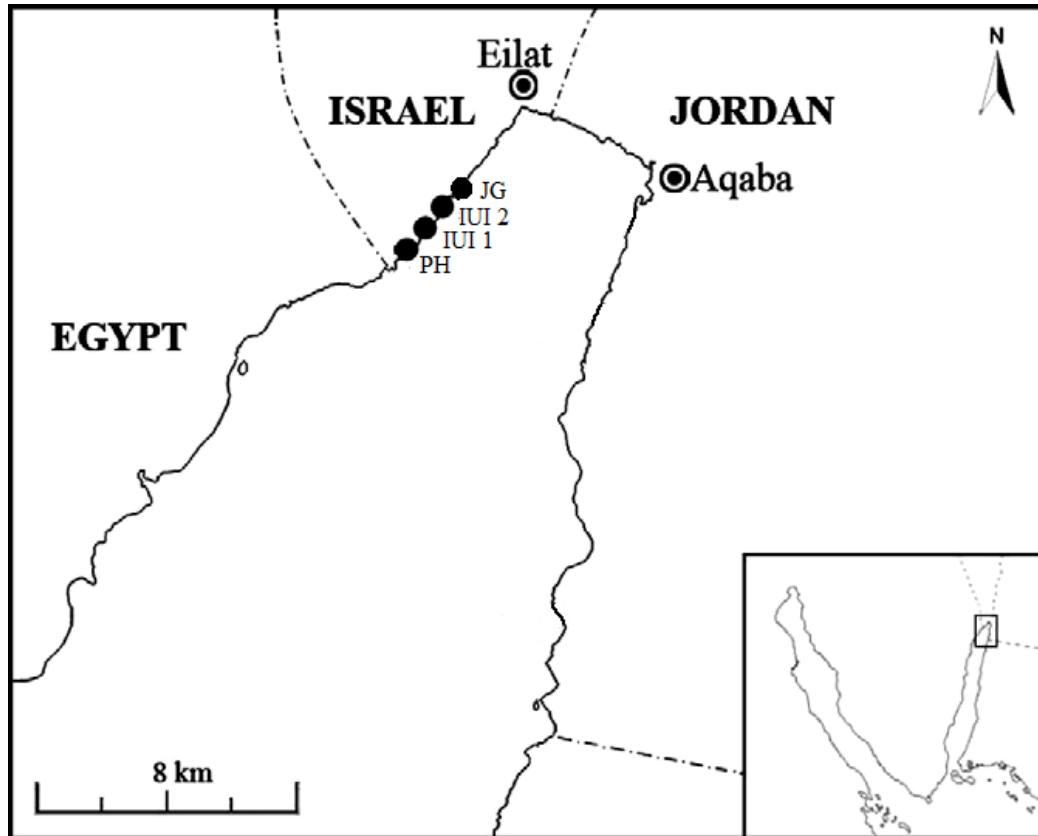
A second objective was to collect data on fish behaviour that can be used to develop improved methods of abundance estimation (Chapter 5).

3.4. Material and Methods

3.4.1. Study Area

The study was carried out at four sites in the Gulf of Aqaba (Fig 3.1). The southernmost site was opposite the Princess Hotel (PH) and characterised by isolated outcrops of coral interspersed with sea grass beds (*Halophila stipulacea*). Site IUI1 was in front of the Inter-university Institute for Marine Sciences in Eilat (IUI), where a continuous reef habitat extends down to 65 m (Brokovich et al. 2008, Brokovich et al. 2010). IUI2 was also in front of IUI however slightly North of the pier and consisted of a sandy slope with limited coral cover. Japanese Garden (JG), was the most northerly site and is part of the Coral Reserve, a 3.5 km long stretch of continuous reef habitat. At the study sites the main habitat was patchy coral and sand.

Figure 3.1. Map of the sites of UVC and BUC surveys; Japanese Garden (JG), IUI 1, IUI2 and Princess (PH)..



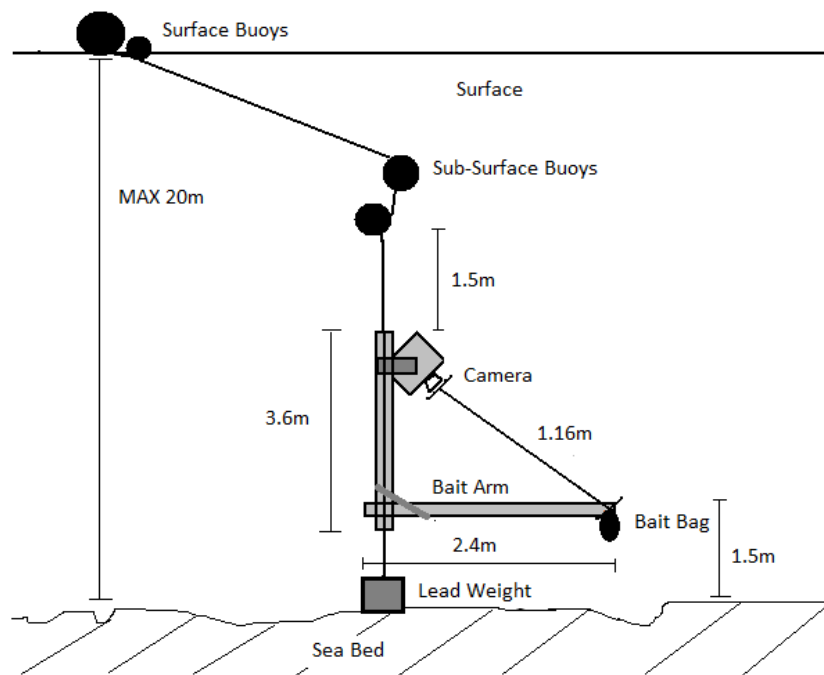
3.4.2. Baited Underwater Camera System

A housed Sealife DC800 digital compact camera was mounted facing outwards at an angle of 60° from vertical towards a bait bag suspended 1.5 m above the sea bed (Fig. 3.2). No lighting systems were necessary due to the high light penetration and good visibility experienced at all sites and depths.

The bait consisted of 100 g of coarsely chopped *Sparus aurata* and *Dicentrarchus labrax* contained in a fine mesh bag. The camera was positioned so that the bait was in the centre of the field of view and was replaced between each deployment to ensure that the strength of the bait plume at the start of each deployment remained consistent. The camera frame was weighted at the bottom with a 5 kg lead weight and kept upright in the water with two subsurface buoys, attached 1.5 m above (Fig. 3.2). A dive timer was

attached to the frame to record the time that the system remained on the sea floor and the maximum depth that it reached. The field of view was approximately 4 m² surface area of the reef and extended to a height of approximately 2 m into the water column depending on the topography.

Figure 3.2. Diagram of the BUC system as was deployed and retrieved from the boat. When deployed by a diver surface buoys were replaced by a lifting bag attached to the frame.



3.4.2.1. Deployment Methods

The camera was set to record images every 30 s for a deployment duration of 1 h. A variety of methods were used to deploy the camera system, which depended upon the depth and survey area. In areas where the descending weight was unlikely to cause damage (areas with limited coral cover) deployments were made from a small hard boat. The camera system was lowered into the water over the side of the boat, weight first, as soon as the desired depth was located by the boat's echo sounder. Once the camera had been deployed the boat left the area to minimise disturbance. The system was recovered by hand hauling using the mooring line. Some of the areas surveyed had relatively dense cover of fragile coral, and a condition of the research permit was that divers deployed the

system by hand. A lift bag was attached above the sub-surface buoys before the BUC was passed from the boat to the divers in the water. The divers descended with the camera system, to place it on an area of sand at the planned depth. The lift bag was then removed and the divers left the area. Recovery was made at the end of the deployment by reattaching and inflating the lift bag.

A single BUC deployment was made at 5, 10, 15 and 20 ± 1.8 m depth at the 4 sites; IUI1, IUI2, PH and JG to (deployments details in Table 3.1a) to reach a total of 16 deployments. This study involved a paired experimental design to investigate the effect of survey method on predatory fish assemblages and has 16 paired replicate BUC deployments and UVC surveys. Deployments in the same sites were made at least 6 hours apart to ensure that bait plumes from the deployments did not interfere with each other. Deployments were made between the hours of 07:00 and 18:00 from the 31st January to the 11th February 2010.

3.4.3. Underwater Visual Census

Diver transects were conducted to correspond to the BUC surveys (31st January to the 11th February 2010) at IUI1, IUI2, Japanese Garden and Princess Hotel at depths of 5, 10, 15 and 20 m (Table 3.1.b). An area of 2 x 50 m was swum once and the numbers of 10 invertebrate and fish feeder (IFF) species (*Epinephelus fasciatus*, *Variola louti*, *Cephalopholis miniata*, *Cephalopholis hemistiktos*, *Lethrinus mahsena*, *Sufflamen albicaudatus*, *Parupeneus forsskali*, *Parupeneus cyclostomus*, *Gymnothorax spp.*, *Pterois miles*) were specifically recorded using the trophic classification from Khalaf and Kochzius (2002). The time to the observation of the first individual (t_{ob}) from each of the 10 IFF species was also recorded.

Table 3.1. Details of a) baited underwater camera deployments and b) underwater visual census transects in four sites; IUI1, IUI2, Japanese Garden (JG) and Princess (P), in the Gulf of Aqaba.

a)

Site	GPS Position	Date	Start Time	Duration (minutes)	Depth (m)
IUI1	29 30.14N, 34 55.08E	01/02/2010	12:25	60	15
IUI1	29 30.14N, 34 55.08E	02/02/2010	12:25	60	20
IUI1	29 30.14N, 34 55.08E	03/02/2010	08:36	60	5
IUI1	29 30.14N, 34 55.08E	03/02/2010	15:15	60	10
IUI2	29 30.08N, 34 55.05E	03/02/2010	15:19	60	5
IUI2	29 30.08N, 34 55.05E	04/02/2010	08:51	60	5
IUI2	29 30.08N, 34 55.05E	04/02/2010	15:41	60	20
P	29 29.44N, 34 54.30E	04/02/2010	14:42	60	20
JG	29 30.18N, 34 55.07E	07/02/2010	07:22	60	5
P	29 29.44N, 34 54.30E	07/02/2010	12:07	60	15
IUI2	29 30.08N, 34 55.05E	07/02/2010	13:25	60	15
P	29 29.44N, 34 54.30E	09/02/2010	09:29	60	10
JG	29 30.18N, 34 55.07E	10/02/2010	08:02	60	15
P	29 29.44N, 34 54.30E	10/02/2010	10:55	60	5
JG	29 30.18N, 34 55.07E	10/02/2010	16:23	60	20
JG	29 30.18N, 34 55.07E	11/02/2010	07:54	60	10

b)

Site	GPS Position	Date	Start Time	Duration (minutes)	Depth (m)
IUI1	29 30.14N, 34 55.08E	01/02/2010	12:25	4	15
IUI1	29 30.14N, 34 55.08E	02/02/2010	12:25	4	20
IUI1	29 30.14N, 34 55.08E	03/02/2010	08:36	4	5
IUI1	29 30.14N, 34 55.08E	03/02/2010	11:15	4	10
IUI2	29 30.08N, 34 55.05E	03/02/2010	15:19	4	5
IUI2	29 30.08N, 34 55.05E	04/02/2010	08:51	4	5
IUI2	29 30.08N, 34 55.05E	04/02/2010	13:41	4	20
P	29 29.44N, 34 54.30E	04/02/2010	14:42	4	20
JG	29 30.18N, 34 55.07E	07/02/2010	07:22	4	5
P	29 29.44N, 34 54.30E	07/02/2010	12:07	4	15
IUI2	29 30.08N, 34 55.05E	07/02/2010	13:25	4	15
P	29 29.44N, 34 54.30E	09/02/2010	09:29	4	10
JG	29 30.18N, 34 55.07E	10/02/2010	08:02	4	15
P	29 29.44N, 34 54.30E	10/02/2010	10:55	4	5
JG	29 30.18N, 34 55.07E	10/02/2010	16:23	4	20
JG	29 30.18N, 34 55.07E	11/02/2010	07:54	4	10

All BUC deployments had a matching transect at the same location and depth and took place within 10 days of the BUC deployment. Here the aim was to compare the assemblages of IFF species that were recorded by the BUC and UVC surveys using a pairwise comparison. Also to determine the relationship between the maximum number of fish observed at one time (Max_N) and the time of arrival of the first individual (t_{arrival}) at the BUC for each species and density estimates and time to the observation of the first individual (t_{obs}) recorded by the UVC transects.

3.4.4. *Image and Data Analysis*

For each BUC deployment and UVC transect the species diversity and Pielou's evenness index was calculated. Sample-based rarefaction curves were created for each method using Estimate S (Colwell 2005) (Fig. 3.3). A sample-based rarefaction curve computed the number of species as a function of the accumulated number of samples, or surveys, and a steep slope would indicate that many more species remain to be recorded while a

level curve would indicate that most species have been sampled (Colwell et al. 2004). This enabled a comparison to be drawn between the number of UVC and BUC surveys required to survey the 10 IFF species.

The Max_N and t_{arrival} of each species were used as a metric of comparative abundance (avoiding repeated counts of the same individual) for BUC data (Willis and Babcock 2000, Willis et al. 2000). For UVC transect the density (individuals m^{-2}) and the t_{ob} of each species were recorded as metrics of abundance. For each transect or deployment the datasets created were 1) total species richness and evenness, 2) Max_N or density for each species and 3) t_{arrival} or t_{ob} of each species. These datasets are displayed in histograms in Fig. 3.4a and b.

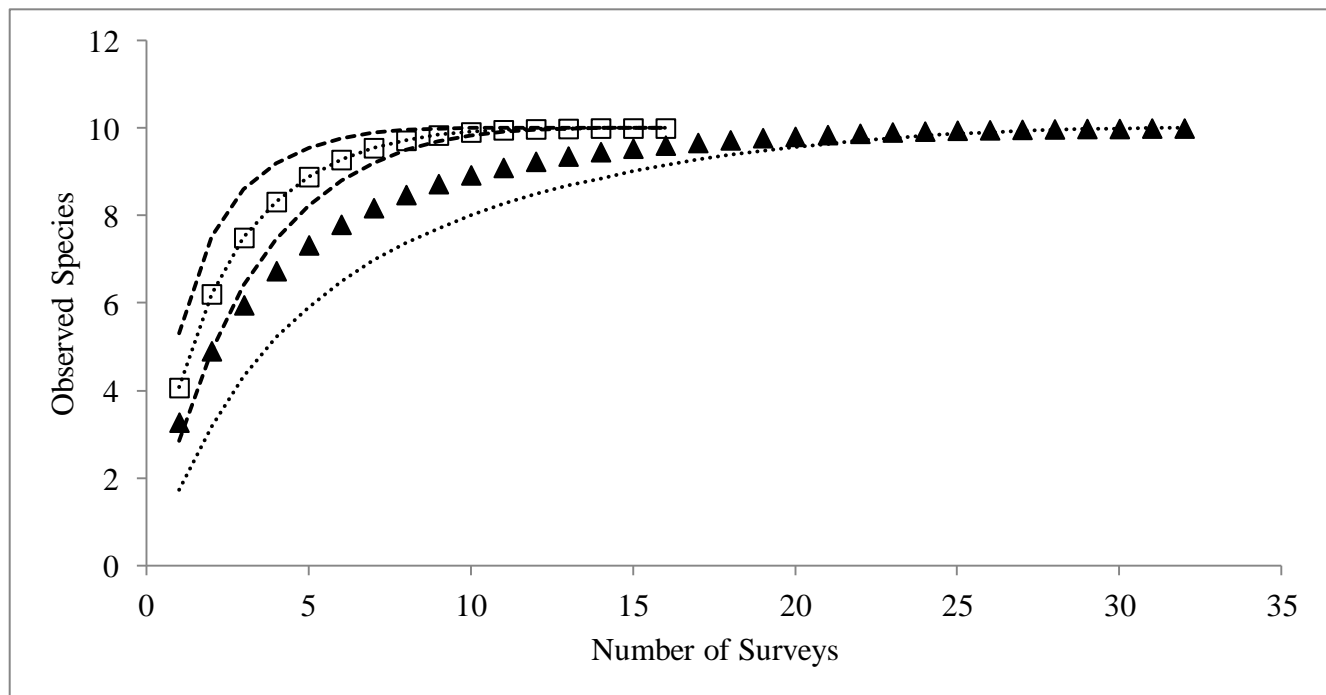
The multivariate statistics package PRIMER (Version 6. Primer-e, UK) was used to explore the data and examine any differences in species composition between survey methods. Data sets were $\log(x+1)$ transformed to ensure that rarer species were accounted for in the analysis. The effect of method (BUC, UVC) on the observed assemblage was visualised using non-metric multi dimensional scaling (MDS) using the Bray-Curtis coefficient of similarity (Fig. 3.5). Differences in assemblage structure recorded by the two methods were explored using a one-way crossed ANOSIM. The R ANOSIM statistic value provides a relative measure of the degree of separation of prior-defined groups by comparing it to randomly assorted data. An R statistic of zero would indicate that there is no separation between the groups, while a value closer to one would indicate that the groups are well separated (Clarke and Gorley 2006). A SIMPER analysis was also preformed to examine the role of individual species in the average Bray-Curtis dissimilarity between any assemblages that differed significantly between recording methods (Clarke and Warwick 2001) (Table 3.2). Analysis of the different IFF assemblages observed by each method enabled hypothesis two to be tested.

The existence of any correlations between the Max_N and t_{arrival} recorded in BUC surveys and density and time to first observation in UVC for 10 IFF species was examined using a Spearman Rank correlation in the statistical programme R. This was to determine whether the BUC Max_N and t_{arrival} reflected the density or t_{ob} of IFF assemblages recorded by the UVC and to test hypothesis one (Table 3.3 a – j and Fig. 3.6).

3.5. Results

Both survey methods recorded all 10 of the IFF species. The BUC surveys recorded a mean species richness of $4.33 \text{ species} \pm 0.29 \text{ IFF deployment}^{-1}$ and the UVC transect $3.28 \text{ species} \pm 0.10 \text{ IFF transect}^{-1}$. A mean Pielou's evenness measure of 0.87 ± 0.06 and 0.86 ± 0.03 were recorded for the IFF assemblages by BUC and UVC respectively. The rarefaction curve shows that the full range of 10 IFF species present were detected in 12 BUC deployments, while 32 UVC transects were required to reach this total (Fig. 3.3).

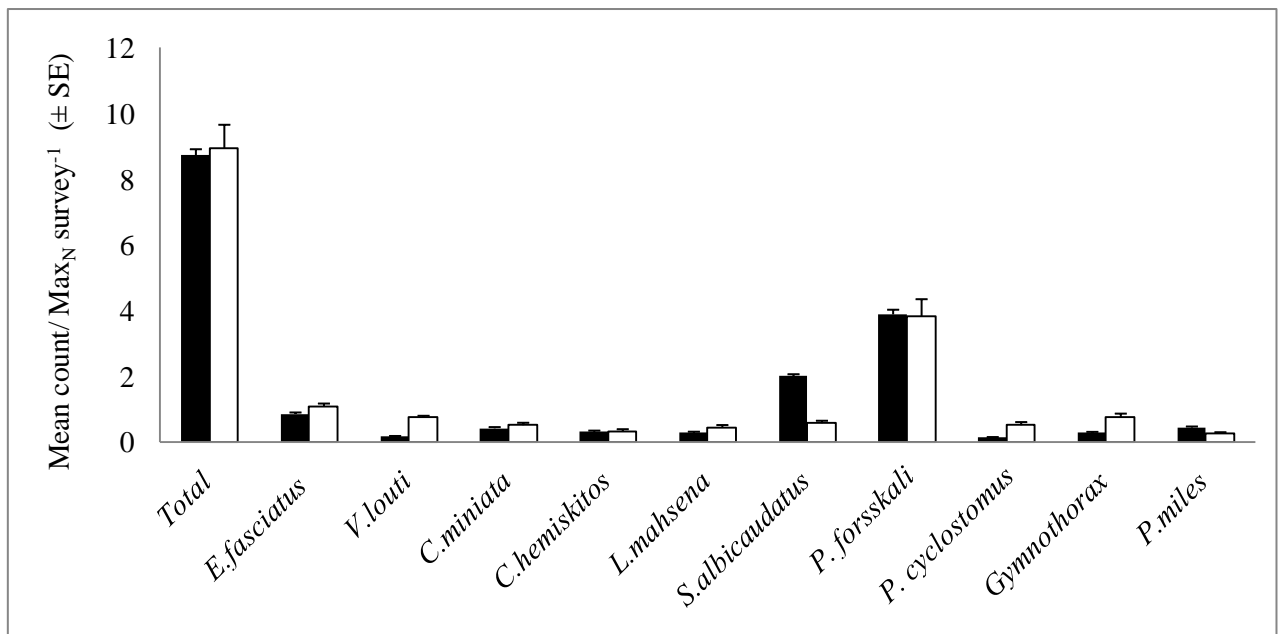
Figure 3.3. Sample based rarefaction curve of the total number of predatory species (IFF) ($\pm 95\%$ CI) recorded by BUC (\blacktriangle), 95 % CI upper and lower bounds (---), and UVC (\square), 95 % CI upper and lower bounds (..) survey methods. Curves calculated using the Mao Tao estimator in Estimate S (Colwell et al. 2004).



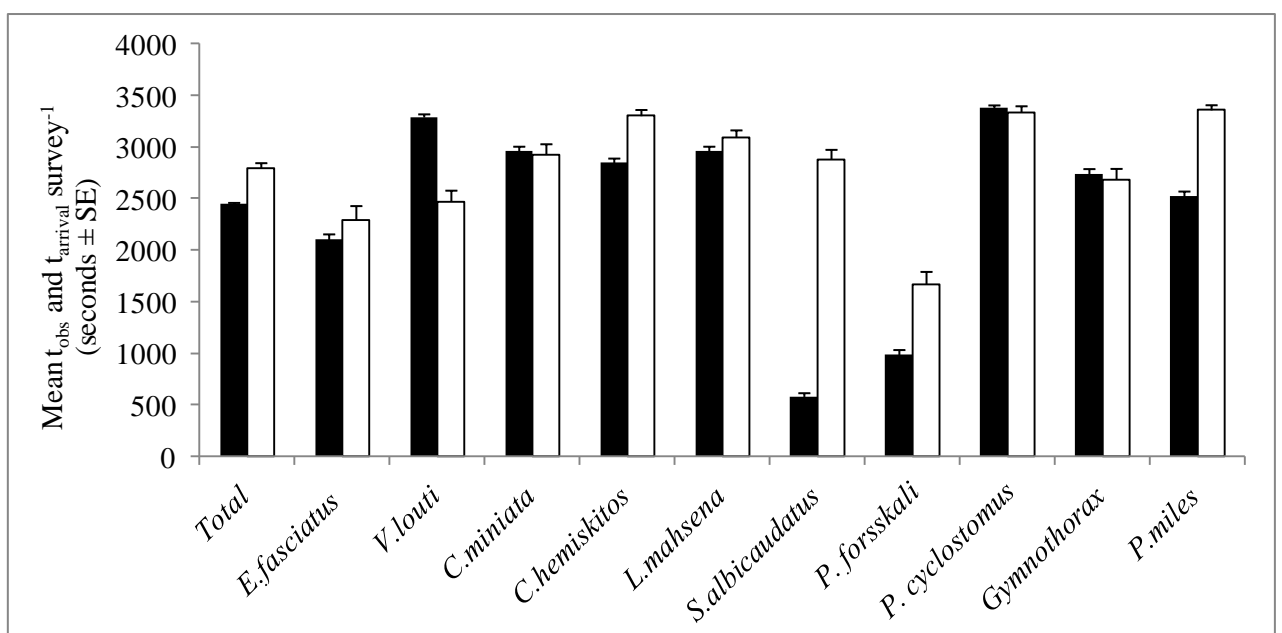
The UVC transects recorded 8.72 IFF individuals \pm 0.19 IFF transect⁻¹ (mean \pm SE), while BUC surveys observed 8.94 individuals \pm 0.57 deployment⁻¹ (Fig. 3.4a). The mean time to the first observation of a fish from the IFF species in the UVC was 2755 seconds \pm SE 10.3 transect⁻¹ and the time to the first arrival of an individual from the IFF species in the BUC was 2451 seconds \pm SE 5.2 deployment⁻¹ (Fig. 3.4b).

Figure. 3.4. a) Mean (\pm SE) underwater visual census (UVC) counts or maximum number of fish observed at once (Max_N) at the baited underwater camera (BUC) and b) UVC time to first observation (t_{obs}) and time to first arrival (t_{arrival}) of individuals from the 10 invertebrate and fish feeding species (Khalaf and Kochzuis, 2002a) recorded by the UVC (solid bars) and BUC (open bars) surveys.

a)



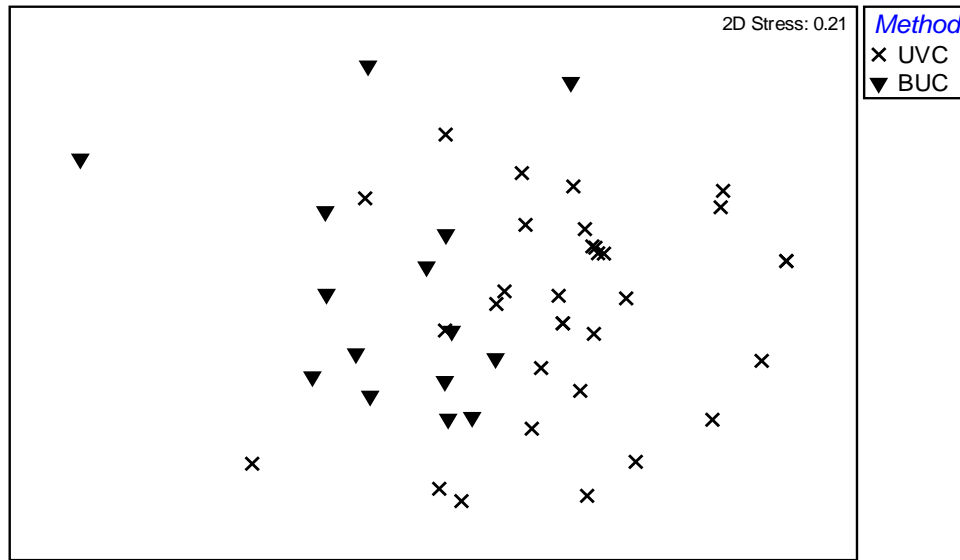
b)



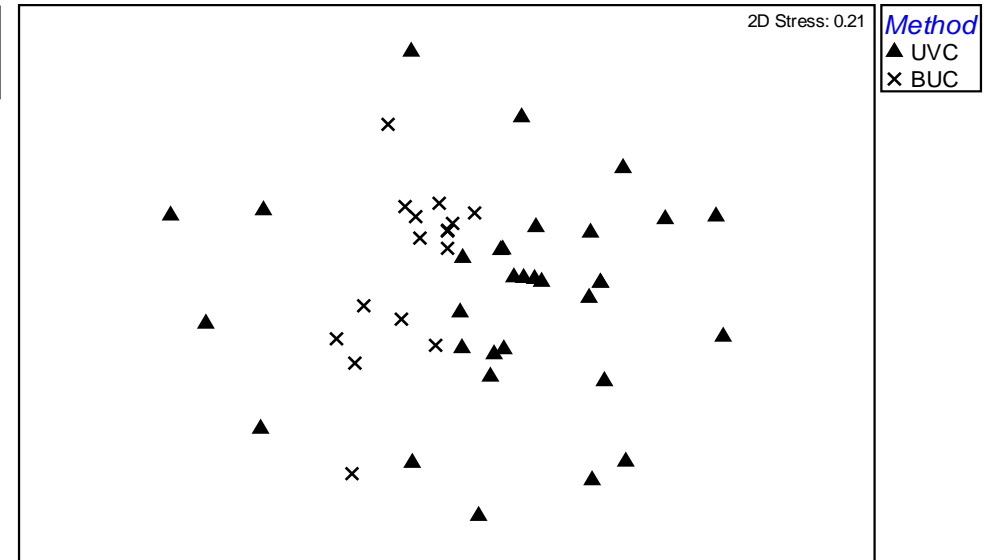
There was no significant difference between the IFF assemblages recorded by the two methods for either BUC Max_N vs. UVC density (ANOSIM, $R = -0.02$, $P = 0.48$) or BUC t_{arrival} vs. t_{obs} (ANOSIM, $R = 0.11$, $P = 0.06$). This was also illustrated in the MDS plots which do not show any patterns of clustering of data collected by individual survey method (Fig. 3.5).

Figure 3.5. Bray-Curtis similarity and Multi-Dimensional Scaling (MDS) analysis to compare a) the mean maximum number of individuals (Max_N) and density b) the first arrival time (t_{arrival}) and the time of first observation (t_{obs}) of fish recorded by the baited underwater camera system (BUC) and underwater visual census (UVC) surveys.

a)



b)



When Max_N and UVC population density were compared using SIMPER the contribution of *P. forsskai*, *E. fasciatus*, *Gymnothorax spp.*, *C. miniata*, *V. louti* and *C. hemistikos* to the assemblage was higher in BUC Max_N data than in UVC population densities (Table 3.2). The contribution of *S. albicaudatus* was greater in UVC surveys. Similar results when the assemblages were weighted by BUC t_{arrival} and UVC t_{obs}. Only *V. louti* made a higher contribution in BUC data than to UVCs.

Table 3.2. Species, ranked in order of importance, contributing to the average dissimilarities between invertebrate and fish feeding fish assemblages recorded in baited underwater camera (BUC) deployments and underwater visual census (UVC) surveys, as determined by similarity percentages (SIMPER) analysis based on a) the maximum number of individuals (Max_N) and density b) the time to first arrival (t_{arrival}) and time to first observation (t_{obs}).

a)

UVC and BUC

Average Dissimilarity = 92.82

Species	Av.abund (UVC)	Av.abund (BUC)	Av.Diss	Diss/SD	Contri%	Cumm%
<i>Parupeneus forsskali</i>	0.27	0.36	24.77	1.40	26.68	26.68
<i>Sufflamen albicaudatus</i>	0.26	0.19	15.92	1.22	17.15	43.83
<i>Epinephelus fasciatus</i>	0.19	0.23	15.37	1.14	16.55	60.39
<i>Gymnothorax spp.</i>	0.13	0.22	10.52	1.15	11.33	71.71
<i>Cephalopholis miniata</i>	0.00	0.21	5.85	0.78	6.30	78.02
<i>Variola louti</i>	0.00	0.19	5.19	0.82	5.59	83.61
<i>Cephalopholis hemistiktos</i>	0.04	0.14	5.11	0.65	5.51	89.12
<i>Lethrinus mahsena</i>	0.06	0.06	3.88	0.56	4.17	93.30

b)

UVC and BUC

Average Dissimilarity = 12.45

Species	Av.abund (UVC)	Av.abund (BUC)	Av.Diss	Diss/SD	Contri%	Cumm%
<i>Sufflamen albicaudatus</i>	3.86	7.17	2.61	2.23	20.94	20.94
<i>Parupeneus forsskali</i>	4.24	5.66	1.98	1.49	15.89	36.82
<i>Epinephelus fasciatus</i>	5.84	6.16	1.73	1.09	13.90	50.73
<i>Gymnothorax spp.</i>	6.68	6.95	1.13	0.87	9.09	59.81
<i>Pterios miles</i>	6.37	7.58	1.11	0.73	8.92	68.73
<i>Cephalopholis miniata</i>	6.91	7.11	0.96	0.73	7.70	76.43
<i>Variola louti</i>	7.39	6.70	0.96	0.79	7.69	84.12
<i>Lethrinus mahsena</i>	6.96	7.38	0.79	0.66	6.33	90.46

Significant correlations were observed between the BUC Max_N and BUC t_{arrival} and between the UVC density and UVC t_{obs} as would be expected. For most individual species, metrics of abundance from UVC did not correlate with those derived from the BUC. One species was an exception to this; the BUC Max_n for the black tip grouper *E. fasciatus* was significantly correlated with the UVC density ($\rho = 0.4541$, $P < 0.01$) and UVC time to first observation ($\rho = -0.4845$, $P = 0.05$) (Table 3.3 a – j and Fig. 3.6). However, the low ρ value is likely due to the spread of the data and that the significant correlation may be driven by a single point.

Table 3.3.(a – j). Results of spearman rank correlation analysis between the maximum number of individuals (Max_N) and the time to first arrival (t_{arrival}) recorded in baited underwater camera (BUC) surveys and density and time to the first observation in underwater visual census (UVC) for 10 invertebrate and fish feeding (IFF) species in the Gulf of Aqaba (significance in **bold**).

a) *Epinephelus fasciatus*

Factors		S	P-value	rho
BUC Max_N	UVC Density	2978.30	0.009	0.4541
BUC Max_N	UVC t_{obs}	8097.76	0.005	-0.4841
BUC Max_N	BUC t_{arrival}	9553.48	<0.0001	-0.7510
BUC t_{arrival}	UVC Density	6297.57	0.410	-0.1594
BUC t_{arrival}	UVC t_{obs}	4315.23	0.251	0.2091
UVC t_{obs}	UVC Density	10591.26	<0.0001	-0.9412

b) *Variola louti*

Factors		S	P-value	rho
BUC Max_N	UVC Density	5574.18	0.9063	-0.0216
BUC Max_N	UVC t_{obs}	5377.24	0.9375	0.0144
BUC Max_N	BUC t_{arrival}	9555.82	<0.0001	-0.7514
BUC t_{arrival}	UVC Density	6060.44	0.5461	0.1208
BUC t_{arrival}	UVC t_{obs}	4796.84	0.5101	-0.1107
UVC t_{obs}	UVC Density	10886.59	<0.0001	-0.9953

c) *Cephalopholis miniata*

Factors		S	P-value	rho
BUC Max _N	UVC Density	5912.79	0.6487	-0.0837
BUC Max _N	UVC t _{obs}	4360.79	0.2706	0.2007
BUC Max_N	BUC t_{arrival}	10655.50	<0.0001	-0.9530
BUC t _{arrival}	UVC Density	4861.10	0.5525	0.1090
BUC t _{arrival}	UVC t _{obs}	6646.09	0.2304	-0.2181
UVC t_{obs}	UVC Density	9344.17	<0.0001	-0.7126

d) *Cephalopholis hemistiktos*

Factors		S	P-value	rho
BUC Max _N	UVC Density	4560.72	0.3695	0.1641
BUC Max _N	UVC t _{obs}	6220.77	0.4442	-0.1402
BUC Max_N	BUC t_{arrival}	10851.48	<0.0001	-0.9889
BUC t _{arrival}	UVC Density	6457.81	0.3144	-0.1836
BUC t _{arrival}	UVC t _{obs}	4575.97	0.3778	0.1613
UVC t_{obs}	UVC Density	10893.66	<0.0001	-0.9966

e) *Lethrinus mahsena*

Factors		S	P-value	rho
BUC Max _N	UVC Density	4666.62	0.4295	0.1447
BUC Max _N	UVC t _{obs}	6513.38	0.2879	-0.1938
BUC Max_N	BUC t_{arrival}	10768.21	<0.0001	-0.9738
BUC t _{arrival}	UVC Density	6906.02	0.1415	-0.2658
BUC t _{arrival}	UVC t _{obs}	3675.2	0.0683	0.3264
UVC t_{obs}	UVC Density	10864.43	<0.0001	-0.9913

f) *Sufflamen albicaudatus*

Factors		S	P-value	rho
BUC Max _N	UVC Density	6218.35	0.4456	-0.1397
BUC Max _N	UVC t _{obs}	4852.53	0.5467	0.1106
BUC Max_N	BUC t_{arrival}	10762.48	<0.0001	-0.9726
BUC t _{arrival}	UVC Density	4779.80	0.4992	0.1239
BUC t _{arrival}	UVC t _{obs}	5839.42	0.7023	-0.0727
UVC t_{obs}	UVC Density	7557.31	0.0295	-0.3851

g) *Parupeneus forsskali*

Factors		S	P-value	rho
BUC Max _N	UVC Density	6575.99	0.2597	-0.2053
BUC Max _N	UVC t _{obs}	5227.21	0.8197	0.0419
BUC Max_N	BUC t_{arrival}	8770.03	0.0002	-0.6074
BUC t _{arrival}	UVC Density	5527.72	0.9431	-0.0131
BUC t _{arrival}	UVC t _{obs}	4684.08	0.4399	0.1415
UVC t_{obs}	UVC Density	9130.64	<0.0001	-0.6735

h) *Parupeneus cyclostomus*

Factors		S	P-value	rho
BUC Max _N	UVC Density	4445.75	0.3103	0.1852
BUC Max _N	UVC t _{obs}	6518.32	0.2856	-0.1947
BUC Max_N	BUC t_{arrival}	10178.95	<0.0001	-0.8656
BUC t _{arrival}	UVC Density	6606.05	0.2481	-0.2102
BUC t _{arrival}	UVC t _{obs}	4254.86	0.2260	0.2202
UVC t_{obs}	UVC Density	10909.16	<0.0001	-0.9995

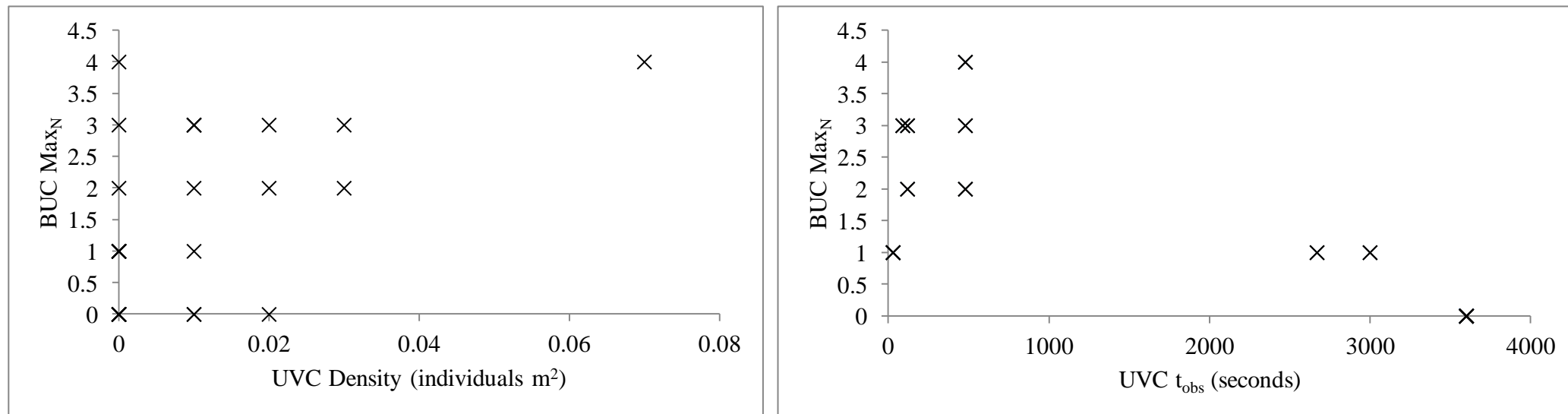
i) *Gymnothorax spp.*

Factors		S	P-value	rho
BUC Max _N	UVC Density	4061.30	0.1579	0.2556
BUC Max _N	UVC t _{obs}	7120.10	0.08947	-0.3051
BUC Max_N	BUC t_{arrival}	10465.35	<0.0001	-0.9181
BUC t _{arrival}	UVC Density	5849.88	0.6946	-0.0722
BUC t _{arrival}	UVC t _{obs}	4868.93	0.5578	0.1076
UVC t_{obs}	UVC Density	10835.47	<0.0001	-0.9860

j) *Pterios miles*

Factors		S	P-value	rho
BUC Max _N	UVC Density	3141.56	0.0789	-0.3659
BUC Max _N	UVC t _{obs}	1464.13	0.0809	0.3634
BUC Max_N	BUC t_{arrival}	4572.12	<0.0001	-0.9879
BUC t _{arrival}	UVC Density	1468.64	0.0827	0.3615
BUC t_{arrival}	UVC t_{obs}	7505.42	0.0341	-0.3756
UVC t_{obs}	UVC Density	4472.10	<0.0001	-0.9444

Figure 3.6. Scatter plot matrix of the significant correlations between the maximum number of individual (Max_N) *Epinephelus fasciatus* per baited underwater camera (BUC) deployment and a) density (individuals m^{-2}) and b) the time to first observation (t_{obs}) of *E. fasciatus* in underwater visual census surveys (seconds).



3.5. Discussion

A similar overall assemblage of the 10 predatory reef fish species was observed by both BUV and UVC survey methods. The full range of predatory fish species could be recorded in a fewer number of BUC deployments compared to UVC transects. For most species Max_N and t_{arrival} did not correlate with population density estimates from UVCs, or with the time taken for divers to observe the first fish of that species (t_{obs}).

Given the potential advantages of BUCs as a survey tool it is unsurprising that their use continues to increase. It is important then that their general limitations are assessed, as well as their usefulness with particular faunas and habitats before the results obtained are used for management purposes. In this study area the results demonstrate that a species list of predatory species can be collected with lower sampling effort using BUCs than UVCs. The cameras could be deployed by non-specialist staff on their way to and from carrying out other work with the resulting images being processed as a batch at a later date. This represents a potentially cost-effective means of collecting qualitative information about the presence of ecologically and economically important species such as groupers and snappers. If stereo cameras were used the data would also provide a means of monitoring the size frequency distributions of these species.

The relative success of BUCs in detecting predators is not surprising given the ecology of many of the species concerned. Several are ambush predators and hide amongst rocks and crevices (Diamant and Shpigel 1985, Gibran 2007) and in the case of moray eels hunt at night (Bshary et al. 2006) which can make them difficult to observe during UVC transect surveys. BUC have been found to be particularly effective at sampling cryptic predators such as *Gymnothorax spp.* which are poorly sampled by UVC and trawling surveys (Cappo et al. 2004, Malcolm et al. 2007). Predatory species will approach the BUC to feed upon the bait where they are more visible making them easier to survey. Predatory species may be also attracted to the BUC by the feeding behaviours of others, as observed by Watson et al. (2005) in BUC deployments in coral reefs in Western Australia, and the congregation of prey species (Cappo et al. 2007). .

Previous studies have found that BUCs to be more cost effective than UVC in terms of time especially as multiple deployments can be made simultaneously to improve

efficiency substantially (Watson et al 2007). A cost-benefit analysis by Langlois et al. (2010) found that stereo baited remote underwater video systems were the most effective sampling methodology for surveying reef fish assemblages in Western Australia. This would allow data on the species present to be collected more frequently, which would be particularly valuable considering the reduced resources available in the region.

Of greater concern though is the lack of correlation for most species between the density of fish observed using UVCs and the commonly-used BUC abundance metrics Max_N and time to first arrival. Max_N in particular is a very widely used metric and the Max_N s for multiple species are commonly combined when calculating diversity indices (Harvey et al. 2007, Zintzen et al. 2012) with the assumption that these are linked to population density. In our study area at least this was not the case and neither BUC metric correlated with UVC data, except for the very abundant grouper *E. fasciatus*. Unless validation has been carried out for the fauna being studied it appears unwise to assume a good relationship between even relative abundance and Max_N .

3.5.1. Differences in Sample Area

The main source of variation between BUC and UVC studies is the area surveyed. This is usually not known for the BUC but is expected to vary according to the current flow and between study species (depending on their swimming speed and behaviour).

Only a few studies have made estimation in areas where current dynamics are known (Watson et al. 2005). The area covered by the plume is unknown for the Gulf of Aqaba making us unable to calculate a measure of fish density from BUC surveys in the same units as the UVC densities. An area-based estimate of plume dispersal using *in situ* current speed measurements and bait dispersal models would be required to enable the surveyed area to be estimated (Heagney et al. 2007). Understanding the true size of this effective survey area remains a major challenge for BUC users, and currently restricts the calculation of true abundance estimates from BUCs to relatively simple topographical and hydrodynamic regimes such as abyssal plain environments (Priede et al. 1990, Collins et al. 2002). Estimation of the number of fish encountering the plume area from fish arrival patterns at the camera also requires information on the fish chemosensory abilities and swimming speed. It has been reported that the mobility of

fish in relation to the survey area is a major influence on the sampling ability of the census method (Samoilys and Carlos 2000). Some predatory species generally have a much greater mobility than other feeding groups, allowing them to search for food over a much larger area than coral associated species (Langlois et al. 2010) and having a greater chance of intercepting a bait plume (Stoner 2004). Deployment to deployment variation in the sample area of the BUCs is the most likely explanation for the poor correlation between BUC abundance metrics and UVC density and t_{obs} .

3.5.2. UVC Density Estimation

Differences between the sampling ability of BUCs and UVC could contribute to the poor correlation between BUC abundance metrics and UVC density and t_{obs} . Individual species behaviours may favour their detection in a single method. Previous studies have found that UVCs can often underestimate cryptic species, which can be easily overlooked by the diver (Cappo et al. 2004). Many of the IFF species examined here are cryptic or ambush predators and their densities could potentially be underestimated in UVC densities. A number of studies have suggested that reef fish species can be repelled or attracted to divers (Cole 1994, Cole et al. 2007). Larger, predatory species, such as *V. louti* and *Gymnothorax spp.*, often display avoidance behaviour towards SCUBA divers which will also reduce their appearance in UVC surveys (Watson et al. 2007, Watson et al. 2010). Behavioural responses to the diver vary between species and will bias UVC density and t_{obs} towards those species attracted to the diver. Studies suggest that the use of BUC removes these behavioural biases (Willis et al. 2000) but the use of bait will introduce their own. An understanding of these behavioural biases will be required to make absolute comparisons between the results from UVC and BUCs. Significant correlations between the BUC Max_N and $t_{arrival}$ of the black tip grouper *E. fasciatus* and UVC transects could be connected to this species being clearly visible during UVCs but also attracted to the BUC. Even though *E. fasciatus* is an ambush predator it usually lies in wait on top of the reef making it visible for UVC surveys. However, even though a significant correlation was reported examination of the correlation shows that a few individual surveys could have a strong influence on the correlation.

Max_N also is a conservative measure of relative abundance, used to avoid repeated counts of the same individual (Willis et al. 2003). However, during UVC surveys individuals that left and returned to the transect could potentially have been counted more than once (Watson et al. 2005). This is unlikely for small, reef-associated predators such as *E. fasciatus* but quite possible for large, mobile species such as *V. louti*. This could lead to an underestimation of fish numbers in BUC metrics and an overestimation in UVCs.

3.5.3. Previous Comparisons

Previous studies comparing the ability of BUCs and diver transects in Western Australian reefs have found that BUCs sample on average a greater abundance and biomass of generalist carnivores at Ningaloo (Langlois et al. 2010) and all species across all habitat types in Hamelin Bay (Watson et al. 2005). In New Caledonia UVC surveys recorded a higher species richness of all reef fish species but the BUC did sample a greater species richness of groupers and emperors (Langlois et al. 2006). These two studies in Western Australia (Watson et al. 2005 and Langlois et al. 2010) made comparisons between BUC Max_N and UVC density by estimating the area the bait plume samples. This was possible due to a detailed knowledge of the current dynamics of the survey areas. However, in both studies no correlation analysis was performed to investigate whether the BUC Max_N (Langlois et al. 2006) or the density estimate derived from the Max_N using estimated plume area (Watson et al. 2005) reflected the density recorded in the UVC. Measures were treated as comparable in further statistical analysis.

Although making up only a small proportion of the fish present, predators have a disproportional impact on the reef community structure (Watson et al. 2007) and also population distribution and abundance reflect changes in fishing pressures through MPA establishment (Russ and Alcala 2003). Therefore the monitoring of the species diversity and abundance of predatory reef fish is important to understand the impact of management and this is relevant to the Eilat Coral Reserve. The BUC method described here would provide qualitative information on the species richness of predatory reef fish in the reserve at low sampling effort. However, information on the abundance of

predatory species is required to understand changes with the available metrics BUCs cannot provide this information.

3.6. Conclusion

In conclusion, BUCs provide a means of assessing predator species richness at low effort but do not provide useful data on abundance. Monitoring using UVCs appears to be the most appropriate means of assessing change in fish abundance at least until improved BUC metrics are developed. While specific to this study area these results indicate that caution should be used when interpreting current BUC abundance metrics unless validation against other methods has been carried out in a similar fauna and habitat.

3.7. Acknowledgements

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4. The impact of iceberg scouring on scavenger diversity, abundance and behaviour in the West Antarctic Peninsula

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4.1. Abstract

Physical disturbance, particularly from iceberg scour, is the major structuring force in polar benthic communities at shelf depths. Scouring kills and damages benthic organisms providing food for the abundant scavenging fauna of coastal Antarctic waters. This trophic group is likely to be strongly affected by changes in iceberg scouring. A baited underwater camera system was used to examine the distribution of scavenging fauna in relation to the spatial variation in exposure to iceberg impacts experienced at different iceberg scouring conditions and depths within Marguerite Bay. The results indicate that different scavenger species are adapted to high and low iceberg scouring environments and that they are distributed in accordance with the recognised pattern of decreasing iceberg scouring frequency with depth. Asteroids dominated the low scoured environment and their relative abundance increased with depth. However, the echinoid *Sterechinus neumayeri* and the nemertean worm *Parbolasia corrugatus* are adapted to high scoured conditions and their relative abundance declined with depth. Iceberg scouring frequency is higher at shallower depths under high scour conditions and the corresponding decline or increase in the relative abundance of individual species begins at a deeper depth. The use of a baited underwater camera system has provided new insights into the macro-benthos scavenger dynamics in the shallow Antarctic environment in relation to ice berg scouring impact.

4.2. Introduction

Physical disturbance, particularly from iceberg scour, is the major structuring force in polar benthic communities at shelf depths (Bergeron and Bourget 1986, Teixido et al. 2004, Barnes and Conlan 2007). When icebergs collide with the sea bed in shallow

coastal waters (<50 m) (Pearse et al. 1991, Dowdeswell et al. 1993, Peck et al. 1999, Brown et al. 2004) they can plough and displace soft marine sediments or abrade rocky substrata (Pugh and Davenport 1997) and are one of the most destructive natural forces affecting benthic environments at depths of < 400 m (Gutt 2001, Smale et al. 2007b). The Antarctic continental shelf is unusually deep, on average 450 m (but up to 1000 m), compared to shelves elsewhere (100 – 200 m), from depression by continental ice sheets and scouring by grounding ice shelves during glaciations (Clarke and Johnston 2003). An estimated 5 % of the Antarctic shelf seafloor (< 500 m) was affected by iceberg scouring over a 14 year period (Gutt 2000, Gerdes et al. 2003).

Grounding frequencies increase with decreasing depth primarily due to there being many small ‘bergy bits’ (size) and few 100 km scale tabular icebergs (Gutt et al. 1996, Barnes 1999, Smale et al. 2007a, b). Keel depth restricts the movement of larger icebergs to deeper parts of the continental shelf (Hequette et al. 1999) and impacts by these larger icebergs are infrequent but of a high intensity due to their greater mass and momentum (Smale et al. 2007a).

Studies of the growth rates of the bivalve mollusc *Yoldia eightsi* indicated that areas at 9 m in a single cove on Signy Island were scoured every 50 – 75 years (Peck and Bullough 1993, Peck et al. 1999). Scouring rates vary seasonally and between years (Brown et al. 2004). Sea ice ‘locks in’ icebergs hindering movement and scouring of the seabed thus the seasonal formation and break up of fast ice (a type of sea ice comprising frozen sea surface joined to the land) causes seasonality in the rate of iceberg scour. Interannual variations in the duration of winter fast ice are negatively correlated with changes in the amount of iceberg scour experienced by coastal habitats (Brown et al. 2004, Barnes and Souster 2011).

Icebergs are calved from glaciers and ice sheets into the marine environment at rates which are strongly seasonal and change between years depending on the state of the “parent” glacier (Barnes 1999, Smale et al. 2007b, Thrush and Cummings 2011). Ice loading, the amount of ice entering the environment, appears likely to increase as the Antarctic environment warms and this increase in loading has the potential to enhance the rate of scouring. Climate mediated losses of fast ice are also likely to increase impacts, for example the scouring rate at Adelaide Island, West Antarctic Peninsula

(WAP), has been measured and has increased by 0.31 scours per m² per year over the last decade resulting in a decline of the longevity of the bryozoans species investigated (Barnes and Souster 2011).

The Intergovernmental Panel on Climate Change (IPCC) confirmed that the WAP is one of the world's three fastest-warming regions (Hansen 2000, Vaughan et al. 2003) and annual mean air temperature changes between 1978 and 2002 in the WAP vary from + 0.22 °C, at Bernardo O'Higgins research station in the Northern Peninsula to + 0.72 °C at Rothera, Adelaide Island, every 10 years (Richard et al. 2012). Overall winter air temperatures in the Antarctic Peninsula have increased by 2° C between 1950 and 2003 (Vaughan et al. 2001, Hall et al. 2010) leading to a reduction of ice sheet area (Pudsey et al. 1994, Vaughan et al. 2003), sea ice duration (Smale et al. 2008) and an increase in glacial retreat (Arrigo et al. 2002, Barnes and Souster 2011, Gutt et al. 2011). Estimated ice sheet losses around the Antarctic Peninsula have increased from $25 \pm 45 \text{ Gty}^{-2}$ in 1992 to $60 \pm 46 \text{ Gty}^{-2}$ in 2006 (Rignot et al. 2008) and in Jan 1995 4200 km² of the Larsen A ice shelf broke up and dispersed, followed by 3200 km² of Larsen B in 2002 (Sane et al. 2012). Fragmenting ice sheets have increased the seaward flow of the glaciers they previously enclosed (Rott et al. 2002, Hall et al. 2010) with 87 % of 244 maritime glaciers studied on the Antarctic Peninsula retreating (Cook et al. 2005, Stammerjohn et al. 2008). The duration of winter sea ice cover in the Antarctic Peninsula and Bellingshausen Sea has reduced substantially with the autumn advance and the spring retreat now on average 2 months later and 1 month earlier respectively than in 1979/1980 (Stammerjohn et al. 2012).

Iceberg scouring causes a significant reduction in benthic biomass and biodiversity on a small spatial scale (Conlan and Kvitek 2005). Reductions of up to 99.5 % of mega and macro-benthos within the area of impact have been measured (Peck et al. 1999, Smale et al. 2007b). Distinct differences in benthic assemblages are apparent between newly impacted and non-impacted sites leading to a mosaic of nearshore benthic communities at different stages of recovery (Barnes and Conlan, 2007, 2012). This promotes between habitat biodiversity (β -diversity) (Gutt et al. 1996, Gerdes et al. 2003, Gutt and Piepenburg 2003), variability of habitat and biological assemblages at both spatial and temporal scales and regional polar benthic diversity (Peck et al. 1999, Smale et al. 2007b).

Ice scouring creates depth-related trends in nearshore polar benthic assemblages. Shallow areas of heavily disturbed sites are characterised by assemblages of low diversity and biomass able to rapidly re-colonise following impacts (Peck et al. 1999, Gutt and Piepenburg 2003, Teixido et al. 2004, Smale et al. 2007a). Intermediate frequencies of ice disturbance are thought to enhance diversity by preventing species domination and creating a patchwork of habitat and communities in various stages of recovery (Brown et al. 2004, Conlan and Kvitek 2005, Smale et al. 2007a). Such communities, representative of intermediate levels of disturbance, were found in areas where ice scouring occurred every 10 years in the High Canadian Arctic (Conlan and Kvitek 2005) and between 5 and 50 m in Antarctica (Peck et al. 1999).

Recent scours are dominated by pioneer species and opportunistic scavengers attracted to feed upon the carrion produced by the impact (Gutt 2001). Mobile scavengers dominated the early recolonisation (by megabenthos) of new scours at Anvers Island (Richardson and Hedgepeth, 1977, McMurdo Sound (Lenihan and Oliver 1995), Signy Island (Peck et al. 1999), Adelaide Island (Smale et al. 2007b, Smale et al. 2007c) and in the Southeastern Weddell Sea (Gerdes et al. 2003).

Clear changes in Antarctic benthic assemblages with depth in the sublittoral environment have been observed by several studies (Barnes 1995, Bowden 2005) and suggested to be largely due to the recognised pattern of decreasing iceberg scouring frequency with depth (Barnes 1995, Barnes 1999).

Scavengers provide an essential ecosystem service by recycling the nutrients and energy enclosed in carrion (Priede et al. 1990, Bailey et al. 2007) and thus probably play a major role in the nearshore environment of much of coastal Antarctica where they are prevalent in the megafauna (Brown et al. 2004, Smale et al. 2007c).

Scavenging is a strategy employed by many mega and macro benthic organisms in Antarctica and many have adopted omnivorous diets to facultatively utilise the carrion produced by scouring impacts (Dayton et al. 1994, Smale et al. 2007c, Gillies et al. 2012). Only mobile fishing gear, such as trawling and dredging, can match the mass of carrion (from benthic community mortality) produced by iceberg scouring (Conlan and Kvitek, 2005).

Despite the apparent importance of ice scouring impact to the dynamics of this dominant group in the Antarctic megafauna there has been limited study of scavenger abundance and behaviour in relation to spatial and temporal differences in scouring impact. Previously a single study has been carried out to examine the colonisation process of scours by scavengers in two heavily ice impacted environments at Adelaide Island, WAP, using an artificial bait representing the carrion from a scouring event (Smale et al. 2007c). Megafaunal aggregations were dominated by the omnivorous asteroids, *Ophionotus victoriae* and *Odontaster validus*, the scavenging/predatory nemertean *Parborlasia corrugatus*, the lysianassid amphipod *Cheirimedon femoratus* and the echinoid *Sterechinus neumayeri* (Smale et al. 2007c). The species composition of the scavengers observed in this study contrasted significantly between the two study sites, only 1 km apart. Smale et al (2007c) suggested that the differences in scavenger composition were linked to the differences in substratum type and exposure to scouring between the sites. Iceberg scouring is predicted to change under conditions of climate change, however the relationships between scouring intensity and scavenger assemblage composition are unknown. It is important to improve our understanding of the scavenging fauna's response to iceberg scouring intensity in order to predict how Antarctic benthic community structure and function might vary under future scenarios where the supply and mobility of icebergs is different.

4.3. Aims and Objectives

4.3.1. Objective 1

The first objective of this study was to investigate how scavenger behaviour, distribution and abundance varied between three depths and at high and low iceberg scouring conditions experienced at four sites in Ryder Bay, Adelaide Island. This expands on the study by Smale et al. 2007c by including two more sites observed to experience lower scouring impact (D. Barnes pers. obs) and three depths thus allowing a study of scavenger assemblage composition over a greater range of scouring intensities and frequencies. This study represents the first examination of how scavengers are affected by the recognised pattern of decreasing iceberg scouring frequency and impact with depth. Data for this investigation was gathered using a novel baited underwater camera (BUC) system.

From consideration of the results of the previous studies the following hypotheses were developed:

- 1) The pattern of scavenger richness and abundance across the depth gradient will vary significantly between the high and low scouring conditions and sites.
- 2) The pattern of individual scavenger species abundance will vary according to their adaptation to either high or low scour conditions.

4.3.2. Objective 2

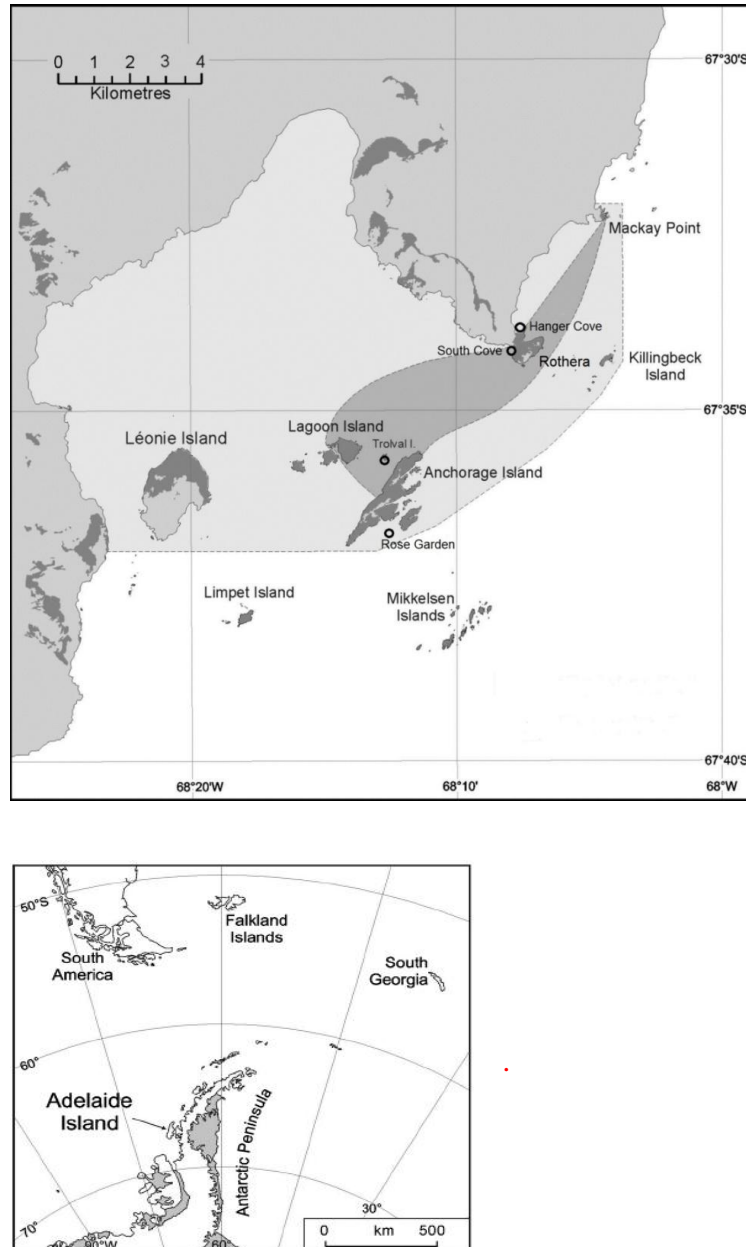
The second objective of this study was to use the BUC to gather data for the development of the modelling methodology discussed in Chapter 5. Such data includes the density of scavengers in the area from photographic underwater visual census (UVC) surveys and the approach swimming speed of scavengers towards the BUC system. The abundance estimates of scavengers recorded by the UVC and BUC model respectively were compared to validate the modelling methodology in Chapter 5.

4.4. Material and Methods

4.4.1. Sites

BUC deployments were made at two sites; Hanger Cove (HC) and South Cove (SC), adjacent to the British Antarctic Survey Rothera Research Station (67°34'07"S, 68°07'30"W), Adelaide Island and at two sites in Ryder Bay; Rose Garden (RG) (67°36'76"S, 68°12'70"W) and Trolval Island (TI) (67°35'70"S, 68°07'50"W) (Fig. 4.1). The area of each site was approximately 0.5 km².

Figure 4.1. Location of Hanger Cove (HC), Rose Garden (RG), South Cove (SC) and Trolval Island (TI) in relation to Rothera Point, Adelaide Island, Antarctica. Insert indicates position of Adelaide Island in relation to the Antarctic Peninsula.



Both HC and SC have a similar bathymetric profile (ca. 30°) (Smale et al. 2007a, Brown et al. 2004) but different substratum. HC has compacted cobbles overlaid with silt, while SC has a mixture of hard bedrock and compacted cobbles (Smale et al. 2007a, c). HC is exposed to the prevailing winds, which bring large numbers of icebergs in during the Summer (Smale et al. 2007c). SC is less exposed to winds but

icebergs are frequently transported in by currents leading both sites to be described as highly scoured by previous studies (Smale et al. 2007a). The frequency and intensity of iceberg scouring has been quantified at both sites using a grid of 25 impact marker blocks placed on the seabed and examined at intervals to determine rates of scouring (Smale et al. 2007a).

The substratum at TI is bedrock, overlaid with sediment and dominated by macro-algae, and RG consists of bedrock with occasional loose boulders and patchy macro-algae. RG and TI were considered to experience low scour conditions from previous observations of the rate of iceberg grounding by BAS scientists and the dense covering of macro-algae, only able to survive under low scouring regimes. The topography present also prevents most icebergs reaching these sites (D. Barnes pers obs). However, scouring regime at RG and TI had not been quantified.

BUC deployments within HC and SC were classified as being in high scour conditions and those in RG and TI in low scour conditions. Within each of the four sites (HC, RG, SC and TI) the locations for three stations were the first three positions from a list of randomly generated coordinates within the designated study area. At each station a deployment was made at 5, 10 and 25 m in a line perpendicular to the contour; resulting in 18 replicate deployments in each scouring condition and 9 at each site and a total of 36 deployments across the four sites. Six replicate deployments were made in each scour condition at each of the three depths (3 deployments at each depth at each site). Deployments timings were made using a rotational matrix which ensured that two deployments were not made consecutively in the same site. This was to allow bait plumes to disperse and to give an opportunity for scavengers to resume their previous behaviours and distributions. The use of the matrix also ensured that all deployments at a particular site or depth were not made at the same time of day. Deployment details are in Table. 4.1.

Table 4.1. Details of baited camera deployments at Adelaide Island, Antarctic. Details on site substratum type are described in 4.4.1.

Site	GPS Position	Date	Start Time	Duration (minutes)	Depth (m)
Hanger Cove	67 33.84S, 68 07.50W	29/12/2011	09:37	90	10
South Cove	67 34.17S, 68 07.84W	31/12/2011	09:52	90	10
Hanger Cove	67 33.84S, 68 07.50W	02/01/2012	09:49	90	5
Rose Garden	67 36.76S, 68 12.71W	02/01/2012	15:09	90	25
Trolval Island	67 35.70S, 68 07.50W	03/01/2012	14:49	90	5
Rose Garden	67 36.76S, 68 12.71W	04/01/2012	09:36	90	5
Trolval Island	67 35.70S, 68 07.50W	05/01/2012	10:28	90	10
Hanger Cove	67 35.70S, 68 07.50W	05/01/2012	15:17	90	10
Rose Garden	67 36.76S, 68 12.71W	07/01/2012	09:51	90	10
Hanger Cove	67 33.84S, 68 07.50W	09/01/2012	10:42	90	25
South Cove	67 34.17S, 68 07.84W	11/01/2012	11:10	90	5
South Cove	67 34.17S, 68 07.84W	13/01/2012	10:17	90	25
Trolval Island	67 35.70S, 68 07.50W	14/01/2012	09:36	90	25
Trolval Island	67 35.68S, 68 13.02W	16/01/2012	09:32	90	10
Rose Garden	67 36.77S, 68 12.88W	18/01/2012	10:21	90	5
Hanger Cove	67 33.85S, 68 07.46W	19/01/2012	09:48	90	5
South Cove	67 34.17S, 68 07.94W	19/01/2012	15:05	90	5
South Cove	67 34.17S, 68 07.94W	20/01/2012	09:25	90	10
Rose Garden	67 36.77S, 68 12.88W	23/01/2012	10:31	90	10
Trolval Island	67 35.68S, 68 13.02W	24/01/2012	14:41	90	25
Trolval Island	67 35.68S, 68 12.79W	25/01/2012	09:51	90	10
Rose Garden	67 36.77S, 68 12.88W	25/01/2012	15:22	90	25
Hanger Cove	67 33.86S, 68 07.50W	27/01/2012	09:45	90	10
Hanger Cove	67 33.85S, 68 07.46W	28/01/2012	09:57	90	25
Trolval Island	67 35.68S, 68 12.79W	30/01/2012	12:22	90	25
Rose Garden	67 36.68S, 68 12.38W	31/01/2012	10:16	90	10
South Cove	67 34.16S, 68 08.00W	01/02/2012	11:12	90	5
South Cove	67 34.16S, 68 08.00W	03/02/2012	10:25	90	10
Trolval Island	67 35.68S, 68 13.02W	03/02/2012	15:33	90	5
Rose Garden	67 36.68S, 68 12.38W	06/02/2012	10:56	90	25
South Cove	67 34.17S, 68 07.94W	07/02/2012	14:58	90	25
Rose Garden	67 36.68S, 68 12.38W	08/02/2012	09:22	90	5
South Cove	67 34.16S, 68 08.00W	09/02/2012	11:29	90	25
Hanger Cove	67 33.86S, 68 07.50W	21/02/2012	11:53	90	25
Hanger Cove	67 33.86S, 68 07.50W	22/02/2012	16:40	90	5
Trolval Island	67 35.68S, 68 13.02W	25/02/2012	09:51	90	5

4.4.2. Baited Underwater Camera System

The BUC system was used to study the arrival of scavengers at a bait and was similar to that described in Chapter 2. Differences however, included that deployments were 90 minutes long due to the slow movements of the Antarctic scavenger species studied, compared to the temperate and tropical fish species studied in chapters 2 and 3. Each bait had a total mass of 200 g (50 g each of freshly chopped *Ophionotus victoriae*,

Odontaster validus, *Sterechinus neumayeri* and *Laternula elliptica*) contained within a mesh bag. This bait was intended to be representative of the local benthic fauna and therefore of the food types made available through iceberg scouring. A SeaLife DC 1000 underwater camera, on an L-shaped aluminium frame, recorded digital stills of the bait at 1 frame every 30 s and was illuminated by two Epoque ES-23DS strobes. A Nortek Aquadopp acoustic Doppler current meter (Aquadopp Current Meter, Nortek, USA) was attached to the vertical element of the frame to record depth, current direction and speed. The frame was held upright in the water column by a sub-surface buoy and was deployed and recovered using a mooring line and surface buoy (Fig. 4.2) for a minimum of 90 minutes. The camera field of view covered an approximate 2 m² area of the seabed however, this would vary slightly with the topography.

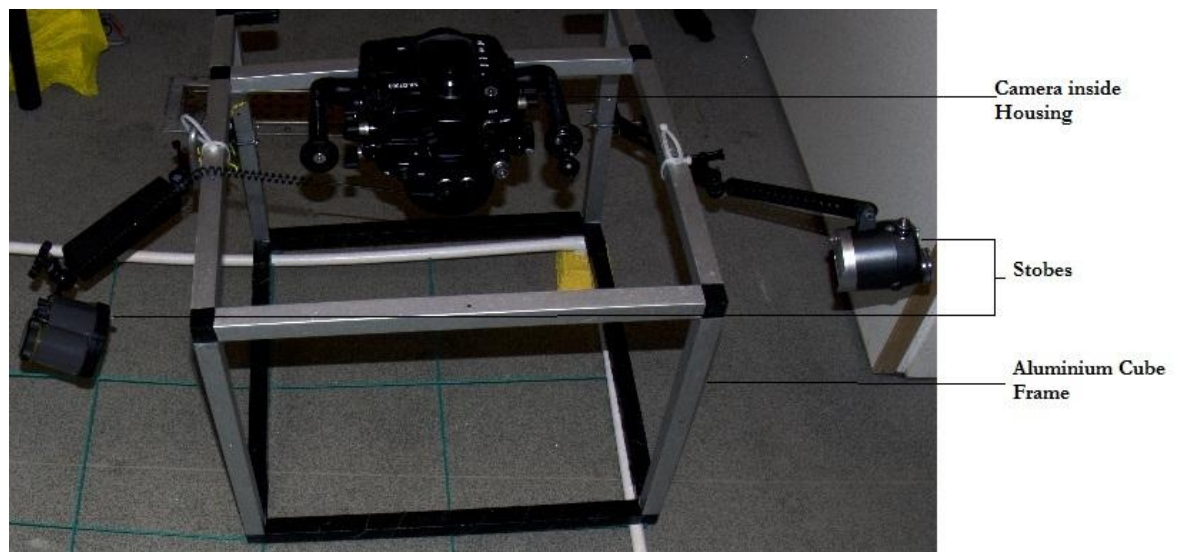
Figure 4.2. Baited underwater camera equipment used to record the accumulation of scavengers at Ryder Bay, Western Antarctic Peninsula, Antarctica.



4.4.3. Stills Transect Methodology

At SC a SCUBA diver used a Nikon D7000 with a Tokina 10 – 17 mm lens in a NA-D7000 Nautican housing and Inon z220 and a Nikon SB-105 strobe to record images of 25 quadrats along a 25 m transect. The quadrat was measured out and marked using a tape. A frame constructed from aluminium box section tubing held the camera at a distance of 40 cm above the seabed while the 50 x 50 cm base of the frame formed the quadrat (Fig. 4.3). Two replicate UVC transects were performed at either side of each of the three replicate BUC deployments made at 5, 10 and 25 m at SC allowing a pairwise comparison to be made between the densities of scavengers observed in the transect and quantified using the model approach detailed in Chapter 5.

Figure 4.3. Camera equipment used to record transect images of macrobenthos assemblages in Ryder Bay, Western Antarctic Peninsula, Antarctica (Image A.Cordingley).



4.4.4. Data Analysis

4.4.4.1. *Baited Underwater Camera Data*

Data on the species and abundance of scavengers observed in the BUC was analysed across the two iceberg scouring conditions; high and low, and the four individual sites; Hanger Cove (HC), Rose Garden (RG), South Cove (SC) and Trolval Island (TI) and

across the three depths 5, 10 and 25 m. At each depth there were 6 replicate deployments for each scouring condition and three for each individual site. However, the iceberg scouring frequency has not been measured at RG and TI and classification as low scoured is based upon years of observations and the habitat type. Also small scale variation in iceberg disturbance has been found at the same site and depths in SC (Smale et al. 2007a) and studies of impact frequency and intensity using impact blocks have found that results can differ substantially between study years. Therefore the diversity and relative abundance of scavenger species recorded by the BUC were also analysed between individual sites. The following statistical tests tested hypothesis one, that the scavenger richness and abundance across the depth gradient would vary significantly between high and low scour conditions and sites.

Species observed in the BUC were categorised into taxonomic groupings (Table. 4.2), some containing a single species, e.g. *Sterechinus neumayeri* was the only Echinoidea. For each deployment the abundance metric; the maximum number of individuals observed at one time in the camera (Max_N) was recorded for each scavenger group. Differences in the scavenger assemblages between iceberg impact condition, depths and sites are compared using differences in the Max_N of scavengers. Initially replicated data of Max_N was $\log(x + 1)$ transformed to down-weight the importance of the highly abundant echinoderm *S. neumayeri*. Data on the number of species, abundance, as measured by the index Max_N , and the Shannon-Weiner diversity index were averaged (\pm SE) for high and low iceberg scouring impact conditions (Tables 4.3 and 4.4, Fig. 4.4) and each site (Tables 4.7 and 4.8, Fig. 4.8) and depth across the six replicate deployments for impact condition and the three replicate deployments for each site.

The response variable Max_N for each scavenger class and the predictors high and low impact condition, depth and the impact condition-depth interaction were modelled using a Generalized Linear Model (GLM). GLMs are particularly useful for modelling count data. Count data can often have a variance greater than the mean, known as overdispersion. Overdispersion was explored in the response variable Max_N by calculating the ratio between the mean and the variance (Table. 4.5). Plots were also examined to determine whether Max_N data contained a large number of zeros (Fig. 4.5). If overdispersion was detected a GLM with a negative binomial distribution was used, which represent models appropriate for the modelling of overdispersed data. The zero-

inflated forms of these models were used in the R package *pscl* if the data were found to contain more than 70 % zeros.

The building of the model using the factors; impact condition, depth and the impact condition-depth interaction, used a backward stepwise selection procedure. This involved introducing all the predictors at the beginning and progressively removing the non-significant ones until all remaining results were significant. The Akaike's Information Criteria (AIC) was used to assess model fit and comparison. Vuong tests are used to compare two regression models to determine which provided the best fit, using the Kullback-Leibler information criteria (KLIC), a measure for the distance between the two statistical models. Diagnostic plots from the best fitting models, based on the AIC score and Vuong analysis, which included the distribution of the model residuals and the normal scores of standardised residual deviance were examined. Examples of the diagnostic plots from the best fitting models for the Asteroid Max_N are displayed in Fig. 4.6. GLM analysis (Tables 4.6) was performed in the statistical programme R and addressed hypotheses 1 and 2. The mean (\pm SE) Max_N for Asteroids, *Ophionotus victoriae*, *Sterechinus neumayeri* and *Parbolasia corrugatus* was plotted in histograms for high and low scouring impact conditions at each of the three sites (Fig 4.7).

The GLM based analysis was repeated using site, depth and the site-depth interaction as predictors of Max_N (Table 4.9) due to the potential for variability in the scouring impact to be present between the sites of the same condition. The mean (\pm SE) Max_N for Asteroids, *O. victoriae*, *S. neumayeri* and *P. corrugatus* at each depth was plotted in histograms for each individual site (Fig 4.9).

Differences in Max_N assemblage were initially examined between impact conditions (high or low), depth (5, 10, 25 m) and impact condition and depth interaction. Differences in assemblage composition were visualised in non-metric multi dimensional scaling (nMDS) plots (Fig. 4.10) and explored using a 2-way crossed ANOSIM (Table. 4.10a) using the Bray-Curtis coefficient of similarity. Pairwise tests were performed to examine the Max_N assemblage between individual depths (Table 4.10b). The same tests were carried out between each pair of sites (HC, SC, TI and RG) and depths (Fig. 4.11. and Table 4.12). A SIMPER analysis examined the role of

individual species in the average Bray-Curtis dissimilarity based on Max_N as an index of relative abundance (Tables 4.11 and 4.13). Analysis of the effect of individual species on the differences between assemblages across the depth gradient under high and low scour conditions and sites enabled differences to be related to individual species adaptations to test hypothesis two.

4.4.4.2. Stills Transect Data

The number of scavengers from each class in each image was quantified using the image analysis software Image-Pro Plus[®] Analyzer (MediaCybernetics). This was converted to density (individuals m^{-2}) by dividing the number of individuals by the transect area (0.5 m^2). This data was used in Chapter 5 to validate the density estimate of Antarctic scavengers produced by the modelled methodology.

4.4.4.3. Scavenger Velocity

The mean velocities of scavengers (*P. corrugatus*, *O. victoriae*, *S. neumayeri*) and Asteroids (*O. validus*) moving towards the bait were estimated by measuring the time taken for individuals to travel across the known camera field of view using Image-Pro Plus[®] Analyzer. Measurements were taken from the full range of sizes of each species visiting the bait and from deployments at all sites and depths and a mean taken to account for the fact that individual speed will be affected by scavenger size. Velocities were included in the development of modelling methodologies described in Chapter 5.

4.5. Results

12 scavenger species from seven taxa visited the BUC, eight fed at the bait and four others approached but were not seen to feed. *P. corrugatus*, *O. validus*, *S. neumayeri* and *O. victoriae* arrived at all sites and depths, however, *O. victoriae* were not seen present at 5 m. Deployments in high and low scour conditions both recorded 8 scavenger species (Table 4.2).

Table 4.2: Scavenger taxa observed feeding directly on the bait (F) or moving towards bait but not seen feeding (T) in baited underwater camera deployment at Hanger Cove (HC), Rose Garden (RG), South Cove (SC) and Trolval Island (TI) at 5, 10 and 25 m.

Class	Species	F/T	Site	Depth (m)
Actinopterygii	<i>Notothenia coriiceps</i>	F	TI	25
	<i>Harpagifer antarcticus</i>	T	HC, SC, TI	10
Anopla	<i>Parborlasia corrugatus</i>	F	All	All
Asteroidea	<i>Odontaster validus</i>	F	All	All
	<i>Cryptasterias turqueti</i>	F	RG, SC, TI	10, 25
	<i>Perknaster aurorae</i>	T	RG	25
	<i>Diplasterias brucei</i>	F	SC	25
	<i>Porania antarctica glabra</i>	T	SC	25
Echinoidea	<i>Sterechinus neumayeri</i>	F	All	All
Malacostraca	<i>Glyptonotus antarcticus</i>	F	RG	25
Ophiuroidea	<i>Ophionotus victoriae</i>	F	All	10, 25
Polychaeta	<i>Flabelligera mundata</i>	T	SC	25

4.5.1. Effects of High vs Low Impact and Interaction with Depth

The mean species richness (\pm SE) of scavengers increased significantly with depth at both high and low scour condition BUC deployments (Table 4.3). In the high scour condition BUC deployments mean (\pm SE) scavenger species richness increased from 2 species \pm 0.6 deployment⁻¹ at 5 m to 3.83 species (\pm 0.39 and 0.61) at 10 and 25 m. Scavenger species richness also increased with depth in deployments in the low impact condition but was higher (however, not significantly) at 5 m (2.83 species \pm 0.39 deployment⁻¹) than in high impact deployments and increased to reach 3.67 species \pm 0.27 at 25 m (Table 4.4 and Fig. 4.4). The mean Max_N of all scavenger species (\pm SE)

also varied significant with depth under high impact conditions (Table 4.3), from $25.83 \pm 8.86 \text{ deployment}^{-1}$ to 73.33 ± 8.88 , in deployments in the high impact condition. While under low scour conditions the mean $\text{Max}_N (\pm \text{SE})$ declined with depth, from mean $66.17 \pm 14.34 \text{ deployment}^{-1}$ to 35.33 ± 7.42 (Table 4.4). The Shannon-Weiner diversity index increased significantly with depth in deployments in both high and low impact conditions (Table 4.3) but in high scour conditions the decline was steeper due to a lower index at 5 m (Table 4.4).

Figure 4.4. Mean ($\pm \text{SE}$) species richness in recorded in BUC deployments in high (open bars) and low (closed bars) iceberg scouring impact.

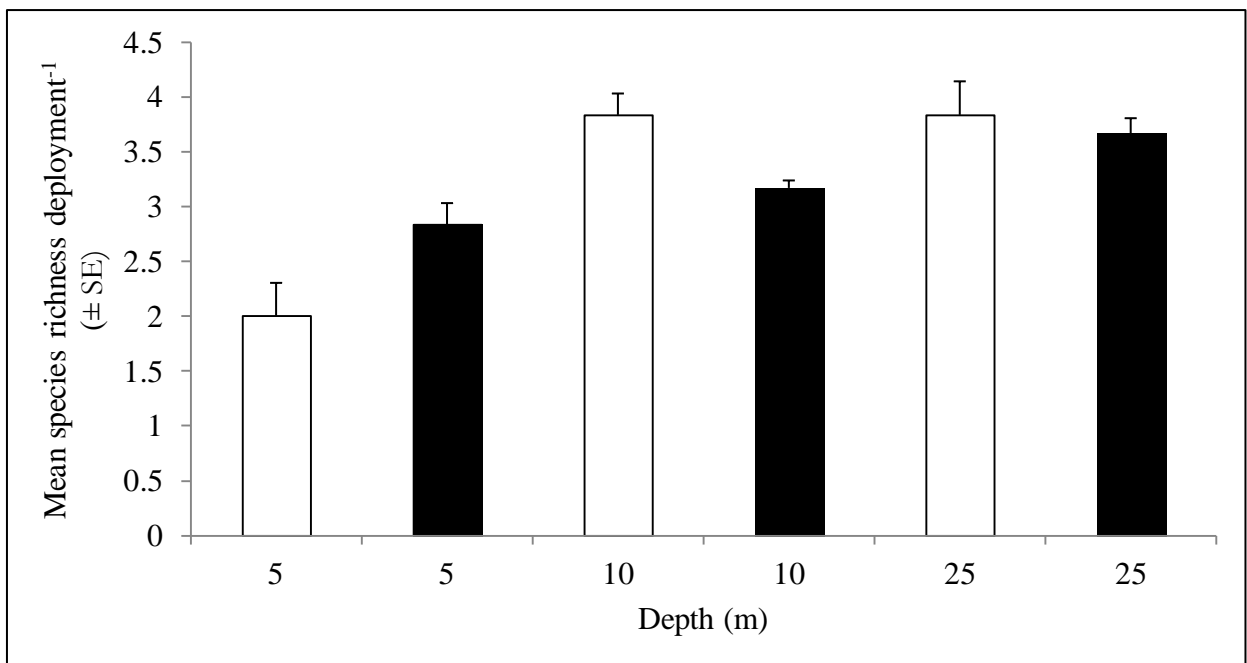


Table 4.3. Results of generalized linear models with either a negative binomial (NB) or linear (L) distribution examining the effect of impact condition (high and low), depth and their interaction on the species richness, total maximum number of individual (Max_N) scavengers at the baited underwater camera at once and the Shannon-Weiner diversity index (significance at $P < 0.05^*$, $P < 0.005^{**}$, $P < 0.0005^{***}$).

Measure	Model	Factor	Estimates	Std. Error	t-value	P-value
Species richness	L	Depth	0.055	0.023	2.408	0.022 [*]
Max _N	NB	Depth	0.227	0.010	2.180	0.029 [*]
Shannon-Weiner	L	Depth	0.017	0.008	2.279	0.029 [*]

Table 4.4. Mean (\pm se) diversity indices; number of species (S), abundance index (Max_N), Pielou's evenness (J') and Shannon-Wiener diversity ($H'(\log_e)$) of scavengers at the baited underwater camera in high and low impact conditions.

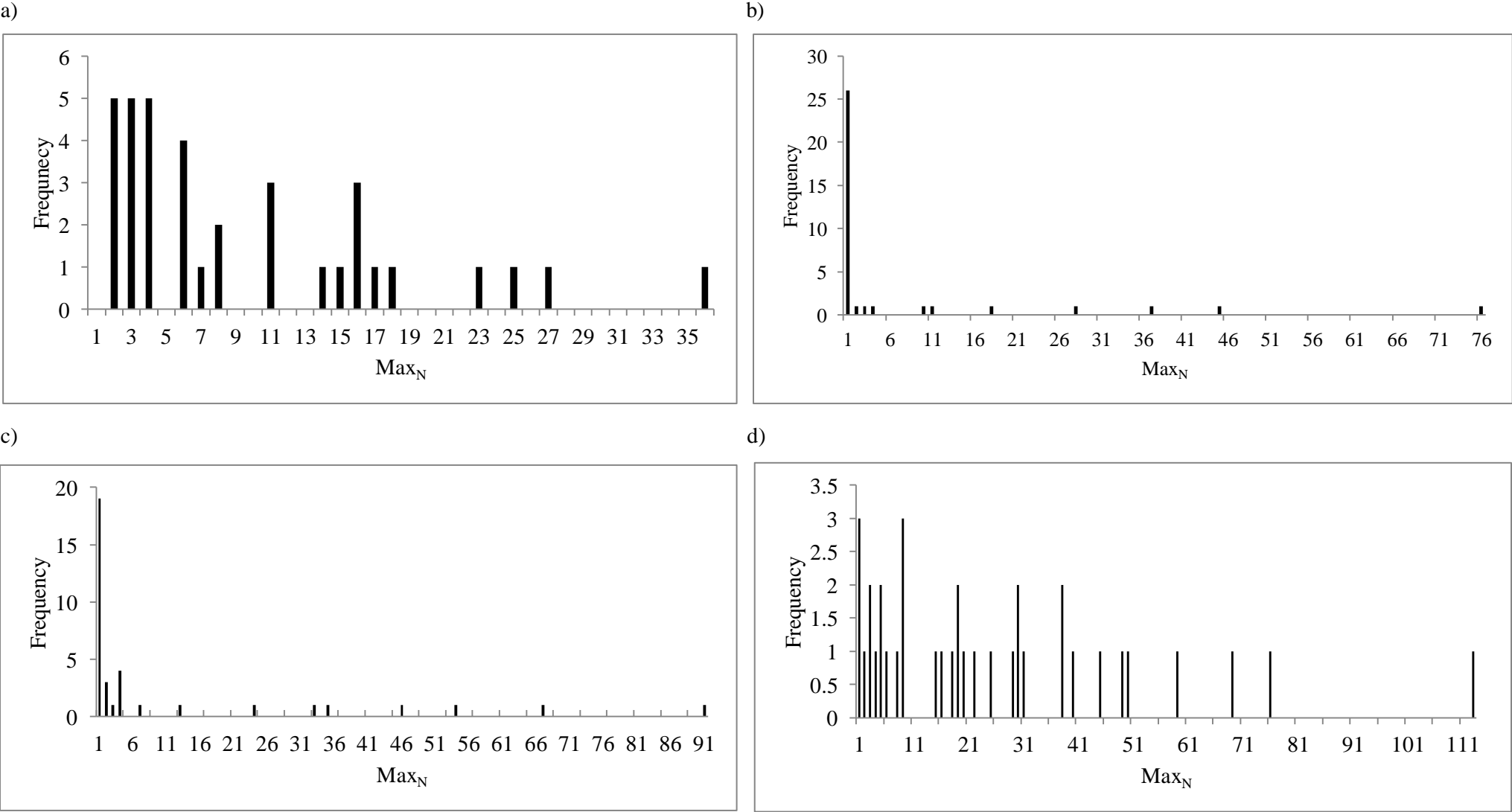
Site/Depth (m)	S	Max_N	J'	$H'(\log_e)$
High 5	2 ± 0.6	25.83 ± 8.86	0.54 ± 0.17	0.34 ± 0.09
High 10	3.83 ± 0.39	64.83 ± 11.57	0.53 ± 0.08	0.72 ± 0.16
High 25	3.83 ± 0.61	73.33 ± 8.88	0.49 ± 0.05	0.82 ± 0.08
Low 5	2.83 ± 0.39	66.17 ± 14.34	0.55 ± 0.08	0.57 ± 0.11
Low 10	3.17 ± 0.14	48.67 ± 16.04	0.69 ± 0.06	0.79 ± 0.08
Low 25	3.67 ± 0.27	35.33 ± 7.42	0.66 ± 0.04	0.86 ± 0.1

Data on the Max_N of individual scavenger classes Asteroids, *O. victoriae*, *P. corrugatus* and *S. neumayeri* was found to be overdispersed from examination of the variance mean ratio (Table 4.5) and *O. victoriae* Max_N contained more than 70 % zeros (Fig. 4.5).

Table 4.5. Mean variance ratio of the maximum number of individuals observed at once in the camera field of view (Max_N) for the Antarctic scavengers; Asteroids, *O. victoriae*, *P. corrugatus*, *S. neumayeri*.

Species	Max _N Variance Mean Ratio
Asteroids	9.09
<i>O. victoriae</i>	39.85
<i>P. corrugatus</i>	44.23
<i>S. neumayeri</i>	25.59

Figure. 4.5. Histograms of the distribution of the maximum number of individuals observed at once in the camera field of view (Max_N) for the Antarctic scavengers; a) Asteroids, b) *O. victoriae*, c) *P. corrugatus*, d) *S. neumayeri*.



Therefore the Max_N data for all scavenger groups studied was analysed using a GLM with either a Negative Binomial (NB) or Zero-Inflated Negative Binomial (ZINB) distribution. The results of the models that fitted the Max_N best are displayed in Table 4.6. Examples of the residual plots of the model fits for Asteroids are displayed in Fig. 4.6.

On examination of individual scavenger classes using the GLM analysis the Max_N of Asteroids in BUC deployments was significantly different between high and low impact conditions as higher numbers were observed in BUCs in low impact conditions. Asteroid Max_N also generally increased with depth in deploymentst in high and low scour conditions but at each depth Max_N was higher in low impact deployments (Table 4.6 and Fig. 4.7a).

From examination of GLM analysis results it was concluded that the Max_N of *O. victoriae* varied significant with depth in deployments under both impact conditions. *O. victoriae* was only observed at 25 m in deployments in the low scour conditions and primarily at 25 m in deployments in the high impact condition (Table 4.6 and Fig. 4.7b).

The Max_N of *P. corrugatus* at the bait varied significantly with depth and a significant interaction factors between scouring condition and depth was observed. The Max_N of *P. corrugatus* decreased with depth in deployments in low scour conditions but peaked at 10 m in deployments in high scour conditions (Table 4.6 and Fig 4.7c).

S. neumayeri Max_N varied decreased significantly with depth in deployments in both high and low iceberg impacts conditions. However, eventhough a significant interaction factor was not observed between condition and site *S. neumayeri* Max_N only declined between 10 and 25 m in high scour conditions due to the low Max_N observed at 5 m (Table 4.6 and Fig. 4.7d).

Table 4.6. Results of generalized linear models with either a negative binomial (NB), zero-inflated poisson (ZIPR) or zero-inflated negative binomial (ZIBR) distribution examining the effect of impact condition (high and low), depth and their interaction on the maximum number of individual (Max_N) scavengers at the baited underwater camera (significance at $P < 0.05^*$, $P < 0.005^{**}$, $P < 0.0005^{***}$).

Species	Model	Factor	Estimates	Std. Error	Z-value	P-value
<i>Sterechinus neumayeri</i>	NB	Depth	-0.051	0.021	-2.451	0.014 [*]
<i>Ophionotus victoriae</i>	ZIBR	Depth	0.225	0.047	4.824	<0.0001 ^{***}
<i>Paborlasia corrugatus</i>	NB	Depth	-0.116	0.049	-2.351	0.019 [*]
		Condition * Depth	-0.189	0.096	-1.965	0.049 [*]
<i>Asteroids</i>	NB	Condition	1.141	0.308	3.711	0.003 ^{**}
		Depth	0.055	0.018	3.121	0.002 [*]

Figure. 4.6. Example residual plots of the GLM analysis examining the effect of site, depth and their interaction on the maximum number of Asteroids at the baited underwater camera. Corresponding data in Table 4.6.

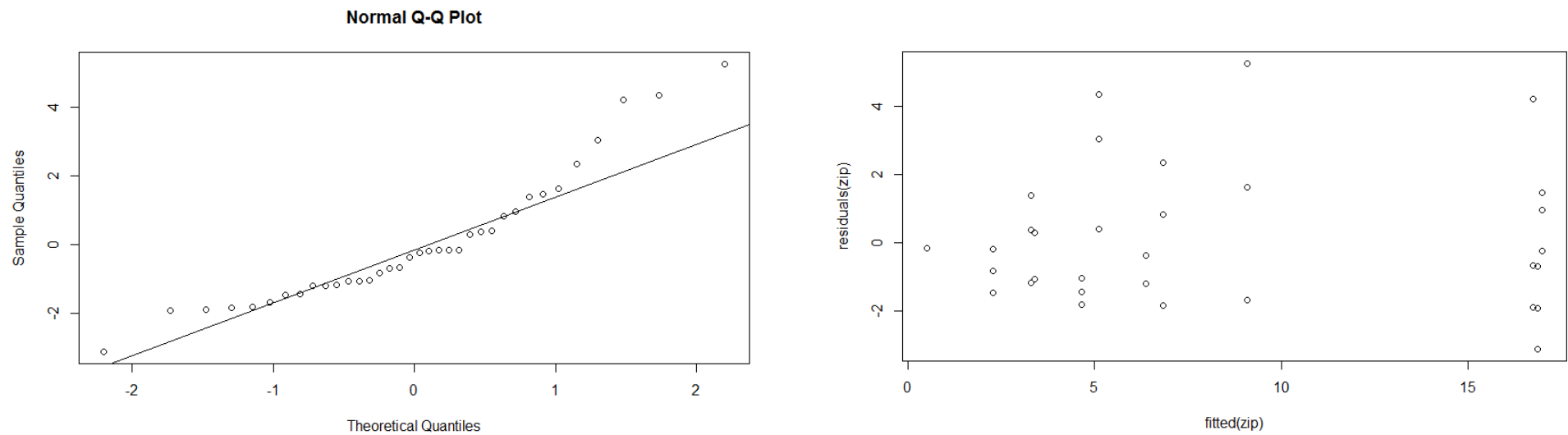
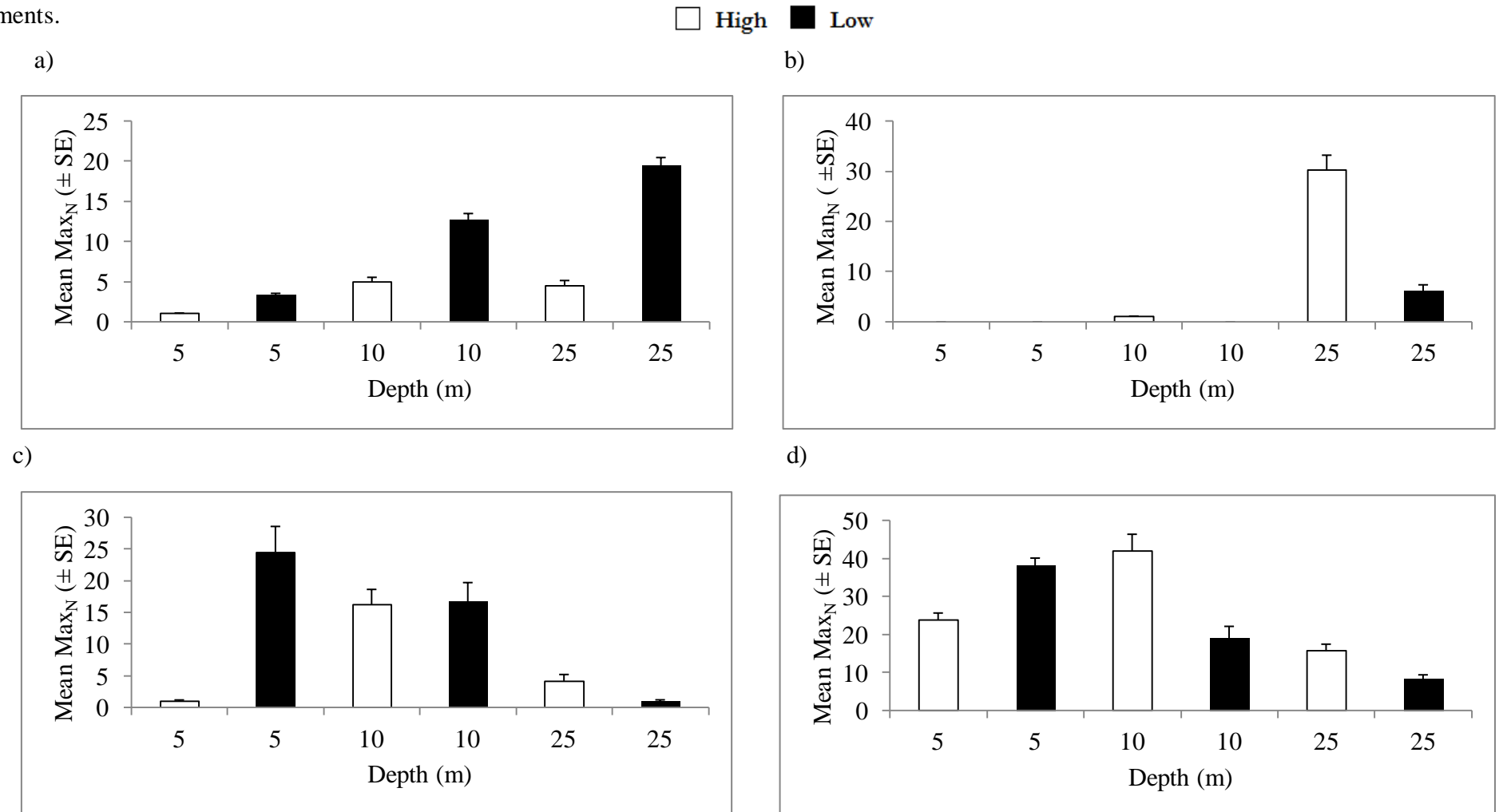


Figure 4.7. Histograms of the mean maximum number of individuals (Max_N), of scavengers a) Asteroids, b) *O. victoriae*, c) *P. corrugatus* and d) *S. neumayeri* at the baited underwater camera at 5, 10 and 25 m at sites experienced high and low iceberg disturbance. Each bar is the mean (\pm SE) of six deployments.



4.5.2. Effects of Site and Interaction with Depth

Diplasterias brucei, *Porania antarctica glabra* and *Flabelligera munda* were only observed present in deployments at 25 m at SC, at which the highest number of species was recorded (5.3 species \pm S.E. 0.19). *Porania antarctica glabra* and *Glyptonotus antarcticus* were only at 25 m at RG (Table 4.2). Mean species richness (\pm SE) varied significant with depth at all sites (Table 4.7). When individual sites were examined species richness increased between 5 and 25 m at RG (from 2 species \pm 0 deployment⁻¹ to 3.33 \pm 0.19) and at SC (2 species \pm 0.33 to 5.33 \pm 0.19) but peaked at 25 m at TI (4 species \pm 0.33) and at 10 m in HC (3.67 species \pm 0.19) (Fig 4.8 and Table 4.8). The mean Max_N (\pm SE) for all scavenger species also varied significantly with depth across all sites (Table 4.7) and increased with depth at RG (from 5 individuals \pm 0.33 deployment⁻¹ at 5 m to 5.67 \pm 0.67 at 25 m) and at SC (from 3.67 individuals \pm 0.38 deployment⁻¹ to 10 \pm 0.88). At HC Max_N peaked at 7.33 individuals \pm 0.84 deployments⁻¹ at 10 m and at TI Max_N was highest at 5 m at 9.33 individuals \pm 0.19 deployment⁻¹ (Table 4.8). The Shannon-Weiner diversity index increased significantly with depth (Table 4.7) and at individual sites increased with depth in RG, SC and TI but peaked at 10 m in HC (Table 4.8).

Figure 4.8. Mean (\pm SE) species richness in recorded in BUC deployments at the four sites; South Cove (SC), Hanger Cove (HC), Rose Garden (RG) and Trolval Island (TI) at three depths 5, 10 and 25 m.

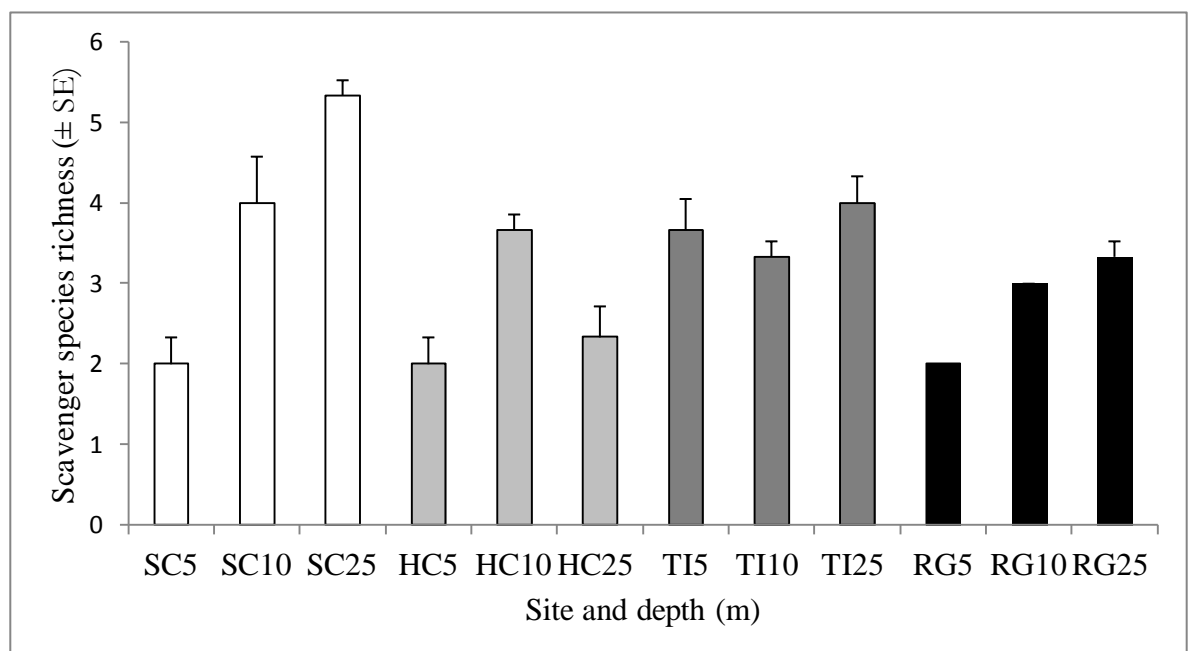


Table 4.8. Results of generalized linear models with either a negative binomial (NB) or linear (L) distribution examining the effect of site, depth and their interaction on the species richness, total maximum number of individual (Max_N) scavengers at the baited underwater camera at once and the Shannon-Weiner diversity index (significance at $P < 0.05^*$, $P < 0.005^{**}$, $P < 0.0005^{***}$).

Measure	Model	Factor	Estimates	Std. Error	t-value	P-value
Species richness	L	Depth	0.055	0.023	2.408	0.022 [*]
Max _N	NB	Depth	0.036	0.017	2.066	0.039 [*]
Shannon-Weiner	L	Depth	0.017	0.008	2.279	0.029 [*]

Table 4.8. Mean (\pm se) diversity indices; number of species (S), abundance index (Max_N) and Shannon-Wiener diversity (H' (loge)) of scavengers at the baited underwater camera at four sites; Hanger Cove (HC), Rose Garden (RG), South Cove (SC) and Trolval Island (TI).

Site	Depth (m)	S	Max_N	J'	H' (loge)
HC	5	2 ± 0.33	4.33 ± 0.19	0.85 ± 0.03	0.51 ± 0.17
HC	10	3.67 ± 0.19	7.33 ± 0.84	0.82 ± 0.03	1.06 ± 0.05
HC	25	2.33 ± 0.38	6 ± 0.88	0.95 ± 0.02	0.70 ± 0.20
RG	5	2 ± 0	5 ± 0.33	0.82 ± 0.05	0.57 ± 0.04
RG	10	3 ± 0	4.67 ± 0.38	0.89 ± 0.3	0.98 ± 0.32
RG	25	3.33 ± 0.19	5.67 ± 0.19	0.88 ± 0.001	1.05 ± 0.05
SC	5	2 ± 0.33	3.67 ± 0.38	0.86 ± 0.03	0.52 ± 0.17
SC	10	4 ± 1.33	8.33 ± 2.78	0.90 ± 0.30	1.21 ± 0.4
SC	25	5.33 ± 0.19	10 ± 0.88	0.88 ± 0.02	1.47 ± 0.04
TI	5	3.67 ± 0.38	9.33 ± 0.19	0.89 ± 0.003	1.13 ± 0.09
TI	10	3.33 ± 0.19	9 ± 0.88	0.93 ± 0.01	1.11 ± 0.04
TI	25	4 ± 0.33	8.33 ± 1.50	0.93 ± 0.02	1.28 ± 0.1

The Max_N of Asteroids was significantly different between individual sites and higher in RG and TI; mean 11.5 individuals \pm SE deployment⁻¹ 0.91 and 12.1 individuals \pm 1.22, than in HC and SC (1 individual \pm SE deployment⁻¹ 0.13 and 6.7 individuals \pm 0.60). Asteroid Max_N also increased with deployment depth in RG, SC and TI but peaked at 10 m in HC as no Asteroids were observed at 25 m (Fig 4.9a and Table 4.9).

O. victoriae Max_N varied significantly with depth at the three sites it was present at and increased from 0 at 5 m to peak at 25 m under high impact conditions at HC and SC (HC mean 8.67 individuals \pm SE 2.83 and SC 51.33 \pm 5.66). *O. victoriae* only arrived at 25 m at deployments in the low scour condition site TI (Fig 4.9b and Table 4.9).

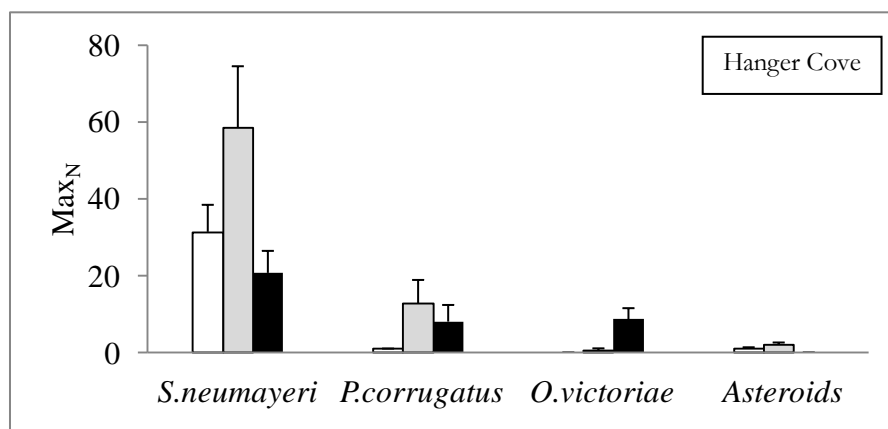
A significant effect of depth and site and depth interaction on the Max_N of *P. corrugatus* in BUC deployments was observed in individuals sites. The Max_N of *P. corrugatus* peaked at 10 m in HC and SC. *P. corrugatus* was however, rare at RG (2 in 9 deployments) and high at TI (27 individuals \pm SE 3.7). Only at TI did *P. corrugatus* Max_N declined from 5 m (mean 49 individuals \pm SE 13.05) to 25 m (1 \pm 0.58) (Fig 4.9c and Table 4.9).

S. neumayeri Max_N varied significantly with depth in deployments in all sites. At high impact conditions experienced at HC and SC *S. neumayeri* Max_N peaked at 10m (HC mean 58 individuals \pm SE 16.04 and SC 25.7 \pm 7.8) but in low impact conditions, at RG and TI, the Max_N of *S. neumayeri* declined with depth (Fig 4.9d and Table 4.9).

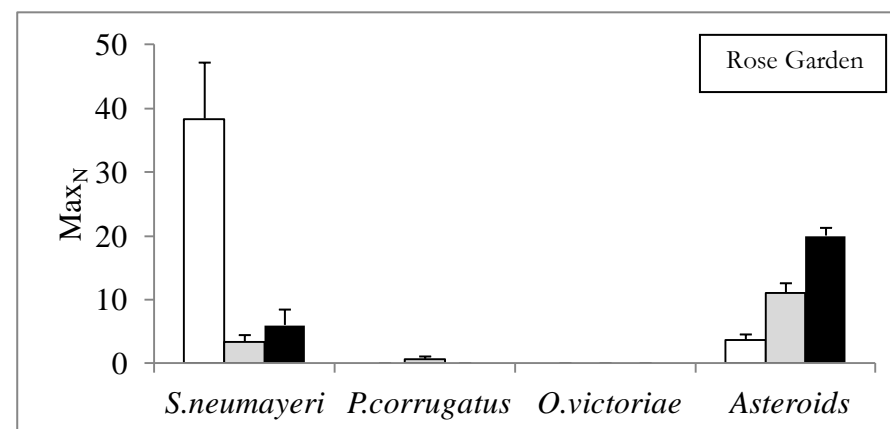
Figure 4.9. Histograms of the mean maximum number of individuals (Max_N), of scavengers at the baited underwater camera at the four sites. Each bar is the mean (\pm se) of three deployments at that site and depth.

□ 5m ■ 10m ■ 25m

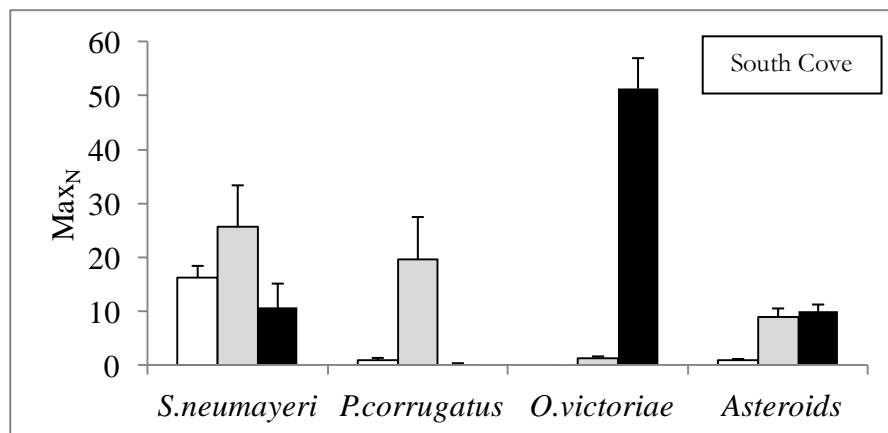
a)



b)



c)



d)

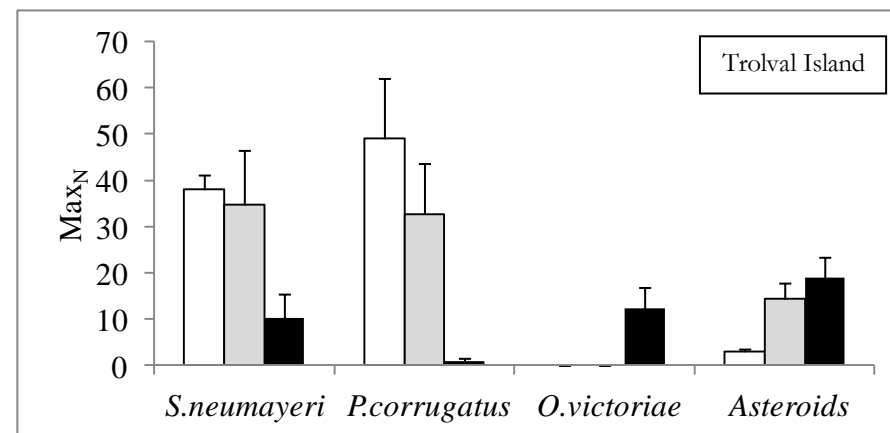


Table 4.9. Results of generalized linear models with either a negative binomial (NB) or zero-inflated negative binomial (ZIBR) distribution examining the effect of site , depth and their interaction on the maximum number of individual (Max_N) scavengers at the baited underwater camera (significance at $P < 0.05^*$, $P < 0.005^{**}$, $P < 0.0005^{***}$).

Species	Model	Factor	Estimates	Std. Error	Z-value	P-value
<i>Sterechinus neumayeri</i>	NB	Depth	-0.051	0.021	-2.451	0.014 [*]
<i>Paborlasia corrugatus</i>	NB	Site	1.352	0.627	2.155	0.031 [*]
		Depth	0.119	0.110	1.082	0.279
		Site * Depth	-0.084	0.041	-2.057	0.040 [*]
<i>Ophionotus victoriae</i>	ZIBR	Depth	0.301	0.122	2.461	0.014 [*]
<i>Asteroids</i>	NB	Site	0.434	0.148	2.928	0.003 ^{**}
		Depth	0.057	0.019	3.009	0.002 [*]

4.5.3. Assemblage: Effects of High vs Low Impact and Interaction with Depth

Bray-Curtis similarity MDS plots (Fig. 4.10) and ANOSIM analysis (Tables 4.10) distinguished between scavenger assemblages in deployments at high and low scouring conditions and depths. Using the Max_N the observed scavenger assemblages (consisting of Asteroids, *O. victoriae*, *P. corrugatus* and *S. neumayeri*) varied significantly between deployments in high and low impact conditions. Depth and the condition-depth interaction also had a significant effect on scavenger Max_N assemblage (Table 4.10a). Pairwise comparisons revealed that there were significant differences between the scavenger assemblages recorded between all three depths (Table 4.10b). The difference between the scavenger assemblages in deployments in high and low scour conditions was dominated by the higher abundance of *P. corrugatus*, *S. neumayeri* and *O. victoriae* in high scour and the Asteroids *O. validus* and *C. turqueti* in low impact condition deployments (SIMPER analysis, Table 4.11a). SIMPER analysis found that *S. neumayeri* and *O. victoriae* were primarily responsible for the differences in scavengers assemblages observed between both 5 and 10 m and 25 m. While between the shallower depths the differences in assemblages (> 80%) was due to *S. neumayeri*, *P. corrugatus* and *O. validus* (Table 4.11b).

Figure 4.10. Bray-Curtis similarity and Multi-Dimensional Scaling (MDS) analysis to compare the mean maximum number of individuals (Max_N) scavengers at the baited underwater camera in high and low iceberg scoured conditions.

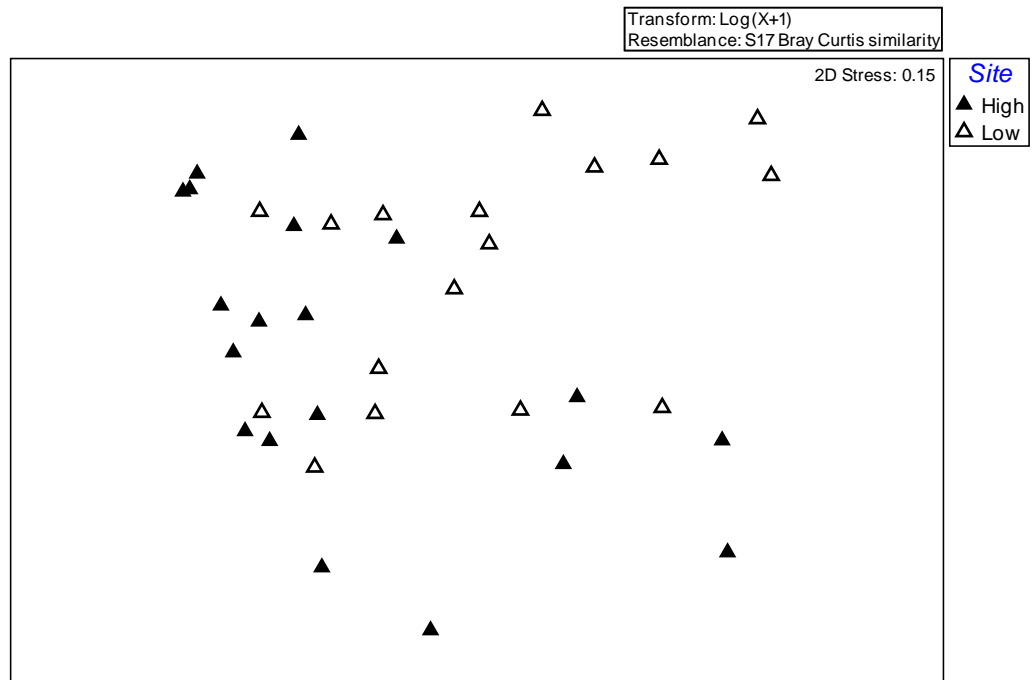


Table 4.10. Results of a 2-way crossed ANOSIM randomised test based on similarity of the maximum number of individual (Max_N) scavengers at the baited underwater camera; a) global test on the effect of high and low impact condition and depth and their interaction and b) pairwise test between depths (significance at $P < 0.05^*$, $P < 0.005^{**}$, $P < 0.0005^{***}$).

a)

	R	P
Condition	0.236	0.008^{**}
Depth	0.338	0.001^{**}
Condition * Depth	0.478	0.001^{**}

b)

Depths (m)	R	P
5, 10	0.237	0.016[*]
5, 25	0.558	0.001^{**}
10, 25	0.182	0.046[*]

Table 4.11. Species, ranked in order of importance, contributing to the average dissimilarities between scavenger assemblages recorded in baited underwater camera deployments in a) Hanger Cove (HC), Rose Garden (RG), South Cove (SC) and Trolval Island (TI) at b) 5, 10 and 25 m, as determined by similarity percentages (SIMPER) analysis based on the maximum number of individuals (Max_N) scavengers at the baited underwater camera.

a)

Average Dissimilarity = 47.13

Species	Av.abund (High)	Av.abund (Low)	Av.Diss	Diss/SD	Contri%	Cumm%
<i>Parborlasia corrugatus</i>	1.23	0.98	10.53	1.02	23.45	23.45
<i>Sterechinus neumayeri</i>	2.89	2.36	10.42	1.14	23.20	46.66
<i>Odontaster validus</i>	1.01	2.23	9.99	1.22	22.26	68.92
<i>Ophionotus victoriae</i>	1.06	0.34	6.52	0.69	14.53	83.44
<i>Cryptasterias turqueti</i>	0.29	0.63	4.04	0.91	9.01	92.45

b)

5, 10

Average Dissimilarity = 37.17

Species	Av.abund (5)	Av.abund (10)	Av.Diss	Diss/SD	Contri%	Cumm%
<i>Parborlasia corrugatus</i>	1.14	1.70	13.61	1.21	35.01	35.01
<i>Sterechinus neumayeri</i>	3.30	2.79	10.53	1.25	27.12	62.16
<i>Odontaster validus</i>	0.97	1.93	7.73	1.30	19.91	82.08
<i>Cryptasterias turqueti</i>	0.06	0.40	2.95	0.62	7.59	89.66
<i>Ophionotus victoriae</i>	0.00	0.26	2.43	0.61	6.25	95.91

5, 25

Average Dissimilarity = 56.55

Species	Av.abund (5)	Av.abund (25)	Av.Diss	Diss/SD	Contri%	Cumm%
<i>Ophionotus victoriae</i>	0.00	1.89	14.94	1.19	26.14	26.14
<i>Sterechinus neumayeri</i>	3.30	1.84	13.98	1.27	24.46	50.61
<i>Parborlasia corrugatus</i>	1.14	0.50	9.32	0.95	16.32	66.92
<i>Odontaster validus</i>	0.97	1.86	8.84	1.62	15.47	82.39
<i>Cryptasterias turqueti</i>	0.06	0.89	5.66	1.15	9.91	92.30

10, 25

Average Dissimilarity = 45.30

Species	Av.abund (10)	Av.abund (25)	Av.Diss	Diss/SD	Contri%	Cumm%
<i>Sterechinus neumayeri</i>	2.79	1.84	11.21	1.42	23.12	23.12
<i>Ophionotus victoriae</i>	0.26	1.89	10.64	1.12	21.95	45.07
<i>Parborlasia corrugatus</i>	1.70	0.50	10.37	1.05	21.39	66.46
<i>Odontaster validus</i>	1.93	1.86	6.37	1.32	13.14	79.60
<i>Cryptasterias turqueti</i>	0.40	0.89	5.28	1.26	10.90	90.50

4.5.4. Assemblage: Effects of Site and Interaction with Depth

A more significant separation of scavenger assemblages between individual sites was found when analysing Max_N using MDS plots (Fig. 4.11) and the ANOSIM (Table 4.12a) analysis. The difference between the Max_N of scavenger assemblages varied most between RG and all other sites. This was primarily due to the unique asteroid rich assemblages at RG (*O. validus* and *C. turqueti*), which was in contrast to the other three sites where scavenger assemblages were dominated by larger numbers of *O. victoriae*, *P. corrugatus* and *S. neumayeri* (Table 4.12b). The Max_N of scavengers observed significantly different between HC and TI and SIMPER analysis revealed that this was mainly due to the larger number of Asteroids (*C. turqueti* and *O. validus*), *P. corrugatus* and *O. victoriae* that arrived in deployments in TI making the assemblages differ from that at HC where few of these scavengers arrived (Table 4.13).

Figure 4.11. Bray-Curtis similarity and Multi-Dimensional Scaling (MDS) analysis to compare the mean maximum number of individuals (Max_N) at the baited underwater camera in Hanger Cove (HC), Rose Garden (RG), South Cove (SC) and Trolval Island (TI) at 5, 10 and 25 m.

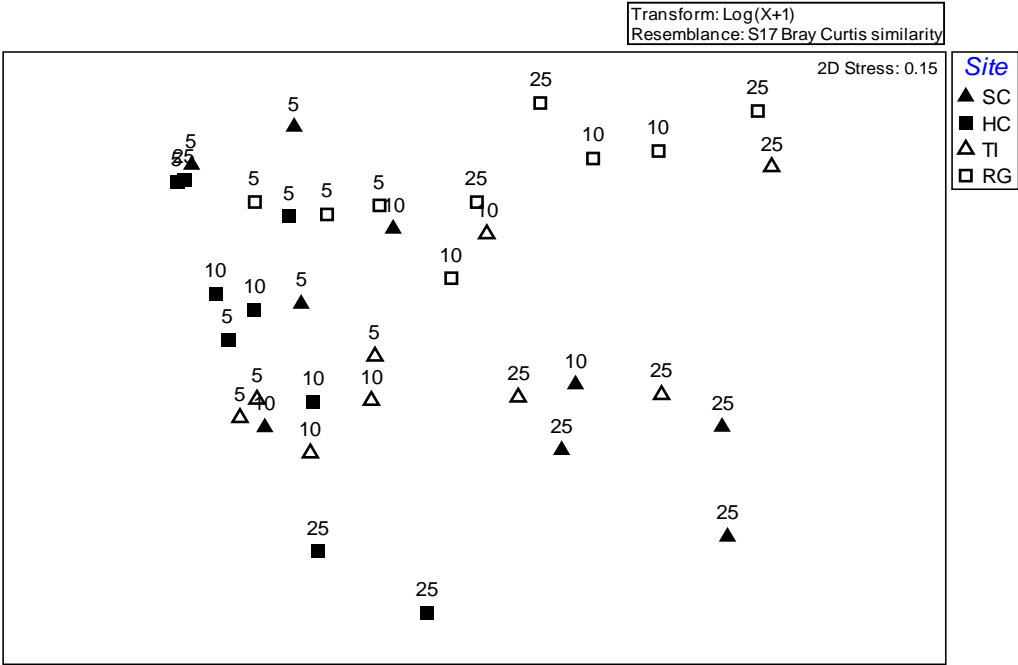


Table 4.12. Results of a 2-way crossed ANOSIM randomised test based on similarity of the maximum number of individual (Max_N) scavengers at the baited underwater camera; a) global test on the effect of site and their interaction and pairwise tests on the effect of b) site; Hanger Cove (HC), Rose Garden (RG), South Cove (SC) and Trolval Island (TI) and c) depth (significance at $P < 0.05^*$, $P < 0.005^{**}$, $P < 0.0005^{***}$).

a)

	R	P
Site	0.364	0.001^{**}
Depth	0.416	0.001^{**}
Site * Depth	0.478	0.001^{**}

b)

Sites	R	P
SC, HC	0.062	0.352
SC, TI	0.012	0.435
SC, RG	0.383	0.045[*]
HC, TI	0.358	0.011[*]
HC, RG	0.519	0.008[*]
TI, RG	0.531	0.018[*]

Table 4.13. Species, ranked in order of importance, contributing to the average dissimilarities between scavenger assemblages recorded in baited underwater camera deployments in a) Hanger Cove (HC), Rose Garden (RG), South Cove (SC) and Trolval Island (TI) at b) 5, 10 and 25 m, as determined by similarity percentages (SIMPER) analysis based on the maximum number of individuals (Max_N) scavengers at the baited underwater camera.

a) HC, TI

Average Dissimilarity = 47.13

Species	Av.abund (HC)	Av.abund (TI)	Av.Diss	Diss/SD	Contri%	Cumm%
<i>Parborlasia corrugatus</i>	1.21	2.22	14.92	1.46	31.67	31.67
<i>Odontaster validus</i>	0.53	2.08	11.09	1.38	23.52	55.19
<i>Sterechinus neumayeri</i>	3.30	2.81	8.71	0.89	18.49	73.68
<i>Cryptasterias turqueti</i>	0.00	0.83	5.87	0.99	12.45	86.13
<i>Ophionotus victoriae</i>	0.70	0.64	4.58	0.56	9.72	95.85

SC, RG

Average Dissimilarity = 43.82

Species	Av.abund (SC)	Av.abund (RG)	Av.Diss	Diss/SD	Contri%	Cumm%
<i>Sterechinus neumayeri</i>	2.37	2.09	10.94	1.32	24.98	24.98
<i>Ophionotus victoriae</i>	1.54	0.00	10.14	0.89	23.14	48.12
<i>Odontaster validus</i>	1.48	2.25	7.76	1.39	17.70	65.82
<i>Parborlasia corrugatus</i>	0.89	0.12	6.97	0.70	15.92	81.74
<i>Cryptasterias turqueti</i>	0.61	0.35	3.43	0.97	7.82	89.56

HC, RG

Average Dissimilarity = 52.42

Species	Av.abund (HC)	Av.abund (RG)	Av.Diss	Diss/SD	Contri%	Cumm%
<i>Odontaster validus</i>	0.53	2.25	16.20	1.69	30.91	30.91
<i>Sterechinus neumayeri</i>	3.30	2.09	15.16	1.43	28.93	59.84
<i>Parborlasia corrugatus</i>	1.21	0.12	9.15	1.01	17.46	77.30
<i>Ophionotus victoriae</i>	0.70	0.00	5.63	0.65	10.74	88.04
<i>Cryptasterias turqueti</i>	0.00	0.35	3.21	0.81	6.12	94.15

TI, RG

Average Dissimilarity = 42.06

Species	Av.abund (TI)	Av.abund (RG)	Av.Diss	Diss/SD	Contri%	Cumm%
<i>Parborlasia corrugatus</i>	2.22	0.12	15.45	1.19	36.74	36.74
<i>Sterechinus neumayeri</i>	2.81	2.09	9.36	1.22	22.26	59.00
<i>Cryptasterias turqueti</i>	0.83	0.35	4.85	1.09	11.54	70.54
<i>Odontaster validus</i>	2.08	2.25	4.41	1.68	10.47	81.01
<i>Ophionotus victoriae</i>	0.64	0.00	4.09	0.50	9.73	90.75

4.6. Discussion

The scavengers visiting the BUC (particularly *O. victoriae*, *O. validus*, *S. neumayeri* and *P. corrugatus*) are common in shallow Antarctic benthic environments subject to ice disturbance (Kidawa 2001, Cranmer et al. 2003) and are known to congregate at scour carrion (Smale et al. 2007c) or bait (McClintock 1994, Thiel and Kruse 2001). The scavenger assemblages recorded by the BUC were significantly different between high and low impact conditions experienced at the four sites; although the majority of the species were common to all sites their relative proportions differed. Different scavenger assemblages occur at high and low iceberg scouring environments and the species within them were distributed in accordance with the recognised pattern of decreasing iceberg scouring frequency and impact with depth.

4.6.1. Scavenger Distribution Under High and Low Scour Conditions

When the relative diversity and abundances of the main scavenger classes was examined using the BUC system the general pattern was that in low impact conditions more slow growing Asteroids were able to thrive and dominate scavenger assemblages while under high impact conditions more pioneer and/or predatory species (*S. neumayeri* and *P. corrugatus*) were present. *S. neumayeri* have a pelagic larval stage with a high dispersal potential allowing them to rapidly established and dominate highly disturbed areas (Nonato et al. 2000, Palma et al. 2007). Benthic assemblages are poorly developed at these highly scoured sites and a high proportion of hard surfaces were bare due to slow recolonisation and growth of assemblages under high scour frequency (Sahade et al. 1998, Gutt 2001) which with high grazing pressures from *S. neumayeri* and *N. concinna* (Bowden et al. 2006) are held at early successional stages (Smale et al. 2007a). *P. corrugatus* has high fecundity, planktotrophic larvae (Heine et al. 1991) enabling it to quickly colonise highly disturbed sites.

Asteroids' relative abundance was greater at low impact conditions. Asteroids have also been reported as common below 15 m at Anvers Island, WAP, where they were only infrequently disturbed by impacts with larger icebergs (Koplovitz et al. 2009). Some of the asteroid species, *C. turqueti* and *D. brucei* have brooding developmental strategies (Pearse et al. 1994, McClintock and Pearse 1986) and require a long

development time and are only able to develop where ice disturbance is infrequent (Nonato et al. 2000, Palma et al. 2007).

4.6.2. Scavenger Distribution with Depth

The pattern of scavenger assemblage distribution in relation to scouring condition is more complex when scavenger distribution is examined across depth profiles. This research is the first investigation of Antarctic benthic scavenger distribution with depth and demonstrates that the distribution of individual scavenger species can be explained by the decline in iceberg scouring frequency with depth. Grounding frequencies decrease with depth primarily due to there being many small icebergs frequently impacting shallow depths (Gutt et al. 1996, Barnes 1999, Smale et al. 2007a, b). Impacts are more infrequent at deeper depths where the keel of most icebergs cannot reach (Smale et al. 2007a). In the low impact condition the frequency of impacts is expected to be relatively low even at the shallowest depths, declining further as depth increases. Several published studies have found that the diversity of Antarctic benthic communities in shallow subtidal areas increases with depth (Smale 2008, Sahade et al. 1998, Nonato et al. 2000). Iceberg scouring has been suggested as a driving force behind the increase in assemblage diversity with depth (Peck and Bullough 1993, Sahade et al. 1998).

4.6.3. Species Richness/Evenness/ Abundance

The general pattern observed by the BUC system was that species richness and evenness of scavengers increased with depth. At the shallow depths, particularly in high scour conditions, only a few highly mobile pioneer species, such as *S. neumayeri* and *P. corrugatus*, are able to quickly re-colonise a scour and persist. However, under low scour conditions a wider range of scavenger species can survive. Contrasting patterns of overall scavenger abundance were however, observed between high and low scouring conditions. The highly abundant *S. neumayeri* dominated assemblages in high scour deployments and was most abundant at shallower depths causing overall abundance to decline with depth. However, deployments in low scour conditions were dominated by Asteroids which are adapted to the low scoured environment and caused overall abundance to increase with depth as scouring frequency declined.

4.6.4. Low Scoured Adapted Species

The ability of individual scavenger classes to withstand iceberg scouring pressure can be used to explain their distribution in relation to the declining frequency of iceberg scouring impact with depth. Asteroids dominated areas experiencing low iceberg scouring frequency and the relative abundance of Asteroids was found to also decline with depth. This pattern was generally observed in deployments in both high and low scoured conditions however, the relative abundance of asteroids was higher in low scoured conditions at each depth. Under low scoured conditions scouring frequency the conditions under which abundant Asteroids assemblages can develop are at a shallower depth than under high scoured conditions. Rich asteroid assemblages were observed at shallow depths in a site in Ryder Bay experiencing low iceberg scouring due to the protection from overhanging crevices (Smale et al. 2008).

4.6.5. High scoured Adapted Species

The opposite of Asteroid distribution with depth can be seen in the relative abundance of *S. neumayeri* and *P. corrugatus*. In low scoured sites the abundance of *S. neumayeri* and *P. corrugatus* peaked at 5 m and declined with increasing depth. *P. corrugatus* is a voracious predator (Heine et al. 1991) and their distribution and abundance was found to be highly dependent upon the availability of prey (Heine et al. 1991). There have been limited studies on the growth of *P. corrugatus* but due to its voracious appetite, high reproductive rate and large size it has been proposed that it has a high growth rate (Heine et al. 1991). *P. corrugatus* will therefore distribute itself where carrion is produced frequently to support this growth rate. In low scour frequency habitats, generally at deeper depths or low scoured sites *P. corrugatus* was almost absent. Here carrion is produced infrequently and biological factors such as competition have a greater impact on the assemblages present causing *P. corrugatus* to be outcompeted by the slower growing carnivore Asteroids (Dayton et al. 1974).

S. neumayeri have been found to be most abundant at shallow depths in previous studies (Smale et al. 2008) and to form dense grazing aggregations at shallow depths where algal densities are high. Dense aggregations of *S. neumayeri* will therefore be

restricted to shallow depths light can penetrate to enable the growth of algal communities. The recruitment strategies of the species allow it to be adapted to survive the high iceberg scouring pressures experienced at shallow depths. *S. neumayeri* has also been observed to approach a simulated carrion and will is therefore likely to also utilise carrion produced from iceberg scours (Smale et al. 2007c).

As well as utilising the carrion from scouring events scavengers can also become carrion themselves. At 5 m in high scoured conditions the frequency of scouring is so high that the death of scavengers by iceberg impact is likely to be common making it difficult for abundant assemblages of *S. neumayeri* and *P. corrugatus* to develop. The short time between impacts also probably means that little benthic biomass can develop, so following impacts there will be relatively little carrion. The pattern of declining abundance with scouring frequency for *S. neumayeri* and *P. corrugatus* therefore begins at a deeper depth under high scour conditions.

O. victoriae was almost exclusively observed at 25 m regardless of scouring condition. A similar observation was made by Nanato et al. (2000) and Palma et al. (2007) at King George Island. *O. victoriae* is a generalist carnivore and its distribution could be affected by the presence of another food source, such as settling phytoplankton (Obermuller et al. 2010) or a physiological adaptation to deeper depths.

4.6.6. Variation Between Individual Sites

A similar pattern of scavenger distribution with iceberg scouring condition and depth were observed when high and low scour conditions were split into individual sites. Both RG and TI have been observed to experience low iceberg impact but significant differences were observed between their scavenging assemblages. At RG *P. corrugatus* was rare and *O. victoriae* absent. However, RG supported rich Asteroid assemblages particularly at 25 m where species, such as *Porania antarctica glabra* and *Glyptonotus antarcticus*, were only seen in this study. Also differences between individual species were observed; *P. corrugatus* relative abundance was very different between the low scour condition sites.

Small scale variation in iceberg disturbance has been found at the same site and depths in SC (Smale et al. 2007a) and studies of impact frequency and intensity using impact blocks have found that results can differ substantially between study years. Contrasting results were found between the studies by Brown et al. 2004 where HC experienced 3 times more scouring events than SC and Smale et al. 2007a who recorded a 1.5 times greater disturbance intensity and frequency at SC compared to HC. This illustrates that as observed between HC and SC a high level of variability in scouring frequency could exist between the two low scoured sites. The distribution of the individual scavenger classes examined in this study would indicate that the frequency of scouring at RG is lower than TI. Possibly scouring is so low at the depths studied that *P. corrugatus* has limited carrion to feed upon and low density communities develop at this site. Richer assemblages of Asteroids are able to develop at shallower depths than TI due to the reduced iceberg scouring frequency experienced at 25 m. Also other species that potentially only survive under very low iceberg impact conditions start to appear in the assemblages (e.g. *G. antarcticus*). Assigning clear levels of impact to each site is therefore problematic even when impact blocks are used, with sites varying temporally as well as spatially in their level of impact. While TI and RG have been assigned to a “low impact” group we do not have a quantitative measure of scouring intensity for these areas and they may differ from each other as much as they do from the high impact sites.

4.6.7. BUC System

This study demonstrates how BUC systems can be used to gather data on a complicated ecological question in extreme conditions where diver based surveys can be very costly and time consuming and often impossible due to adverse weather common in Antarctic climates. The current BUC based study enables data to be collected on the relative abundance of scavenger assemblages between different iceberg scouring conditions experienced at different sites and depths. The generation of absolute abundances from the arrival pattern of Antarctic scavengers at the BUC would enable the system to produce compared data to that currently collected via underwater visual census surveys by divers. This would be useful to generate comparable data on scavenger abundances by a more cost and time efficient means. During the study there were many times when the weather conditions would not permit dive surveys but it was possible to use the

BUC system. The study initially aimed to gather underwater visual census data to correspond to the BUC surveys however it was logistically impossible to conduct dive surveys to match all 36 baited camera deployments. However, corresponding UVC data was collected at one site, SC. Chapter 5 discussed the development of a modelling methodology to generate absolute abundance estimates of Antarctic scavengers from BUC data. Corresponding UVC surveys were used to validate the ability of the methodology to produce abundance estimates comparable to UVC surveys.

4.7. Conclusion

The use of a baited underwater camera system has provided new insights into the macro-benthos scavenger dynamics in the shallow Antarctic environment in relation to ice berg scouring impact. Scavenger populations exhibit a zonation with depth consistent with the established pattern of declining iceberg scouring frequency with depth and individual species distribute themselves according to their adaptation to high or low scour conditions.

4.8. Acknowledgements

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5. Chapter 5

Absolute abundance estimates from shallow water baited underwater camera surveys in the temperate, tropical and Antarctic environments; the presentation of a stochastic modelling approach.

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5.1. Abstract

Baited underwater cameras are becoming a popular tool to monitor fish and invertebrate populations within protected and inshore environments where trawl surveys are unsuitable. Modelling the arrival times of deep-sea grenadiers using an inverse square relationship has enabled abundance estimates, comparable to those from bottom trawl surveys, to be gathered from deep-sea baited camera surveys. Baited underwater camera systems in the shallow water environments are however currently limited to relative comparisons of assemblages associated with areas of differing protection status, habitat and disturbance regime. This study describes a stochastic simulation approach used to model the behaviour of fish and invertebrates around a baited underwater camera system to enable absolute abundance estimates to be generated from arrival patterns. Species specific models were developed for the tropical reef fishes the black tip grouper (*Epinephelus fasciatus*) and moray eel (*Gymnothorax spp.*), temperate fish of the species *Pollachius virens* and the lesser spotted dogfish (*Scyliorhinus canicula*) and the Antarctic scavengers; the asteroid (*Odontaster validus*) and the nemertean worm (*Parbolasia corrugatus*). A sensitivity analysis explored the impact of input parameters on the arrival patterns (maximum number of individuals at the camera at one time, time to the arrival of the first individual and the time to reach maximum numbers) for each species generated by the model. Arrival patterns generated by each model were used to estimate population abundance for the focal species and these estimates were compared to data from underwater visual census transects.

5.2. **Introduction**

5.2.1. *Abundance Estimates from BUC*

Abundance estimates of marine populations, that are both accurate, close to the true abundance of the population, and precise, repeatable under the same conditions, are important to understand changes in marine populations or community (Farnsworth et al. 2007). Accurate and precise measurements will help to achieve sustainable management and effective conservation objectives (Collins et al. 2002). For marine fish and invertebrate populations the majority of this data has been collected using trawl surveys (Fitzpatrick et al. 2012, Johnson et al. 2012). As discussed in detail in the previous chapters trawl surveys are difficult in abyssal environments and unsuitable in marine protected areas or locations with seafloor obstructions (Bailey et al. 2007). Baited underwater camera (BUC) systems have therefore been used in many studies to gather data on deep-sea scavenging fauna (Farnsworth et al. 2007) and fish assemblages in protected areas (Willis and Babcock 2000, McLean et al. 2010). However, to use BUC data to produce absolute abundance estimates of fish and invertebrate populations from arrival patterns requires a detailed understanding of the physical and biological parameters involved in the process of animals detecting and following the bait plume to the camera (Priede et al. 1994, Bailey et al. 2007). The results of Chapter 2 indicate that caution should be used when interpreting current BUC abundance metrics.

Bait plume dispersal from a point source, its detection by fish or invertebrates and their arrival at the source, is influenced by a number of environmental and biological factors (Collins et al. 2002, Stoner 2004). The odour from the bait disperses as a plume into the surrounding water on currents (Reidenbach and Koehl 2011). The velocity and direction of currents will affect the length and lateral dispersal of the plume as well as its dispersal direction (Bailey and Priede 2002, Dorman et al. 2012). Observations of an olfactory plume recorded that stimulus particles were concentrated at the point of source and dispersed down-stream of the current (Montgomery et al. 1999). The release of attractants from the point source begins with a growth phase, followed by a shrinking phase as the release rate declines over time (Collins et al. 2002). The concentration of stimulus within the odour plume decreased with distance from the source (Montgomery et al. 1999,

Reidenbach and Koehl 2011) and with time (Sigler 2000). The dispersal of odour plumes is also affected by turbulence within the aquatic environment (Meager and Batty 2007), the topography over which it travels (Collins et al. 1999, Collins et al. 2002, Reidenbach and Koehl 2011) and the characteristics and persistence of the bait (Bailey and Priede 2002, Stoner 2004).

Fish and invertebrates have evolved olfactory organs with chemosensory abilities that allow them to detect odour plumes when they come into contact with them and follow them to their source (Reidenbach and Koehl 2011). The area within the odour plume where the odour concentration is above the threshold which organisms can detect is known as the 'active space' (Sigler 2000, Stoner 2004). The active space can be affected by the factors described above that influence the physical properties of the bait plume as well as the chemoreceptive abilities of the species or individual (Bailey and Priede 2002). The probability of the fish entering the active space of the bait plume will be dependent on their search behaviours (Dorman et al. 2012), including their swimming speed and position in the water when foraging (Stoner 2004), as well as the abundance and distribution of the population (Armstrong et al. 1992). Foraging in deep-sea grenadiers has been found to include cross-current, sit-and-wait and passive plume detection strategies (Bailey and Priede 2002, Trenkel and Lorange 2011). Active cross-current foraging increases the chance of a the fish encountering the bait plume (Bagley et al. 1994) and is particularly effective when the bait plume becomes elongated and covers a large active space but becomes progressively less efficient as current velocity increases (Bailey and Priede 2002). Once detected, the fish will decide whether to follow the plume based on the feeding motivation that the bait provides (Dorman et al. 2012). This will be affected by the food availability within the surrounding environment (Stobart et al. 2007), as well as the satiation state of the individual (Collins et al. 2002). Other factors such as the reproductive or moult stage, the latter particularly in invertebrates, will impact on the scavenger's decision whether to follow the bait plume or continue foraging elsewhere (Collins et al. 2002). In previous baited studies both fish (Wilson and Smith, 1984, Lokkeborg et al. 1995) and crustaceans (Reidenbach and Koehl 2011) have been observed to follow the bait plume upstream to the source. The rate at which fish or invertebrates arrive at the bait is dependent on both their response time (Dorman et al. 2012), their through-water swimming speed before and after contacting the bait plume (Bailey and Priede 2002) and their search behaviour (Stoner 2004).

The time that individuals remain at the bait will again be influenced by their feeding motivation (Stoner 2004, Stoner et al. 2008). This will be determined by the availability of food within the environment as well as the competition and interactions with other scavengers at the bait (Armstrong et al. 1992, Bailey and Priede 2002).

5.2.2. Deep-Sea Baited Underwater Camera Modelling

The process of bait plume detection, attraction and arrival has been modelled for some deep-sea scavenger species to enable population abundance estimates to be generated from first arrival times at a BUC system (Priede et al. 1990, Bailey and Priede 2002). Models are described in detail in 1.7.3.1.

The arrival times of deep-sea grenadiers at a BUC in two sites in the North Atlantic have been modelled using the methods described in Chapter 1 to produce an estimate of abundance. This was compared to abundance estimates from bottom trawl surveys from approximately the same area and time and a positive correlation was observed between the two abundance estimates (Armstrong et al. 1992, Priede and Merrett 1996). However, BUCs samples were biased towards sampling smaller fish compared to the trawl surveys and the plots of the relationship between BUC and trawl abundance estimates contain a potentially highly influential outlier. Further data from other deep-sea BUC studies has been fitted to the model to provide abundance estimates of deep-sea scavenging demersal fish, for example in other regions of the North Atlantic (King et al. 2008), at three stations off the coast of West Africa (Henriques et al. 2002) and the Mid-Atlantic Ridge (King et al. 2006). The theoretical abundance of *Synaphobranchus kaupii* and *Antimora rostrata* calculated using the BUC arrival time and model from data collected in the North Atlantic did not correspond to abundance estimates from previous trawl surveys. It is thought that the gregarious behaviour of *S. kaupii* violated the assumption of the model. However, the theoretical abundances of *C. armatus* were comparable to those previously observed in the same area (King et al. 2006).

5.2.3. Shallow Water Baited Underwater Camera Modelling

In the shallow water environment however, the development of models of the process of fish or invertebrate arrival at BUCs has been limited (Stoner et al. 2008, Langlois et al.

2012). Heagney et al. (2007) investigated whether abyssal scavenger arrival models could be applied to shallow mid-water baited underwater video data. Models were appropriate for deep-sea BUC studies with long soak times and where scavengers approached more slowly, but not for shallow water BUC studies with much shorter soak times and which attract many fast moving species (Heagney et al. 2007). Compared to the shallow water environment, currents in the abyss are relatively constant, so an assumption of a constant current speed and direction is more suitable (Heagney et al. 2007, King et al. 2008). Abyssal models use a measure of average current speed to model bait plume dispersion to produce estimates of fish abundance (Armstrong et al. 1992, Farnsworth et al. 2007, Stobart et al. 2007). Currents in the shallow water environment however, can be highly variable over small spatial and temporal scales and could generate large differences in the area and fish assemblages sampled (Heagney et al. 2007). The assumptions of deep-sea models also are not capable of accurately describing the complexity of behaviours of shallow water fish species (Ellis and DeMartini 1995, Stobart et al. 2007). Shallow water species often appear more rapidly than abyssal scavengers causing small changes in arrival times to result in large changes in abundance estimates due to the inverse square law of the abyssal model (King et al. 2006, Stobart et al. 2007). The time related metrics used in the deep-sea such as, time to the arrival of the first individual from each species (t_{arrival}) and time to the maximum number of individuals observed at one time (t_{maxN}), have not correlated well with other surveys methods in some shallow water BUC surveys (Stoner et al. 2008). For example, t_{arrival} and t_{maxN} were highly affected by the individual responses of pink snapper (*Pagrus auratus*) and blue cod (*Parapercis colias*) and did not effectively reflect the abundance of the species in and around a New Zealand marine reserve (Willis and Babcock 2000).

The use of BUC systems in shallow waters have enabled relative comparisons of both fish and invertebrate assemblages in the tropical (McLean et al. 2010, Moore et al. 2010), temperate (Willis et al. 2003) and the Antarctic environment (Smale et al. 2007c) between areas of different protection status (Willis and Babcock 2000, Westera et al. 2003), habitat type (Moore et al. 2010, Moore et al. 2011) and disturbance pressure (Smale et al. 2007c). The majority of studies have used the maximum number of individuals, of the same species, appearing in the in-situ of view in any one frame over the whole deployment (Max_N) as an index of relative abundance (Willis and Babcock 2000, Stoner et al. 2008). Max_N avoids the repeated recording of individuals that leave and re-enter the camera in-

situ of view and is a conservative measurement, particularly in areas of high density, as it only represents a proportion of the fish visiting the bait (McClean et al. 2010, Harvey et al. 2012). Some surveys have also used the t_{arrival} and t_{maxN} (Willis and Babcock 2000, Jones et al. 2003). Using various combinations of these three abundance indices have been used in BUC studies to make comparisons between areas protected from fished and open areas. For example, in McClean et al.'s (2010) study of the abundance and size of *Lethrinus miniatus* between the protected and open areas of the Houtman Albrolhos Islands and Westera et al.'s (2008) examination of the impact of the Ningaloo reef sanctuary, Western Australia, on reef fish assemblages. Other shallow water BUC studies have used these indices to examine the impact of habitat on fish assemblages, for example in the Cape Howe MPA, Victoria, Australia (Moore et al. 2010) and for examining the habitat associations of Caribbean reef sharks (Bond et al. 2012).

The area sampled by the active space of the odour plume is largely unknown in shallow BUC surveys. Concerns have been raised regarding the effect of localised environmental conditions, such as topography and current conditions, on plume dynamics making it difficult to make comparisons between areas (Watson et al. 2009). Surveys assume that a comparable area is sampled by each deployment, however, this will often be untrue if current conditions vary (Heagney et al. 2007). The importance of the currents on the dynamics of bait plume dispersal and subsequent fish arrival patterns have been highlighted in several studies in the mid water (Heagney et al. 2007) and demersal environments (Dorman et al. 2012). The unknown sample area of shallow water BUC surveys also makes it difficult to make comparisons with abundance estimates from other survey methods. The plume area sampled by abyssal BUCs is estimated in the modelling approach of Priede et al. (1990) by describing the spreading of the bait plume at the observed current velocity using an odour plume spreading factor. Several studies have investigated the differences in fish and invertebrate studies recorded by BUC and UVC surveys (Langlois 2006, Watson et al. 2010), however, conclusions regarding comparisons have been difficult as the area sampled cannot be directly compared (Langlois et al. 2010).

BUC systems have been found to attract a wide range of shallow water fish and invertebrate scavenger species. The ability and desire to detect and respond to an odour plume will differ substantially between species (Stoner et al. 2008, Watson et al. 2009, Dorman et al. 2012) and it is therefore important to understand species-specific responses

to the odour plume and the BUC system to enable accurate abundance estimates to be generated (Stoner 2004, Stobart et al. 2007). Deep-sea models to estimate demersal scavenger abundance were based upon and worked well for the grenadier (*C. armatus*), which exhibits independent foraging behaviour. However, when applied to the arrival pattern of a species that can be gregarious, i.e. *Synaphobrancus kaupit*, the resultant estimates did not fit well with those from trawl surveys (King et al. 2006). This further illustrates the advantage in developing species-specific models that are based on information from studies of foraging behaviour. The results of chapter 2 highlight that an understanding of the behavioural biases associated with the arrival patterns of fish at the BUC system are required to make absolute comparisons between the results from established methods, such as UVC, and BUCs.

5.2.4. Modelling Approaches to Shallow Baited Sampling Issues

A model to determine the absolute measures of shallow water fish or invertebrate abundance from arrival patterns at a BUC would involve developing an area based bait dispersion model using in-situ measurements of current speed and direction (Heagney et al. 2007). Species-specific models have been recommended to represent the different foraging strategies and movement patterns that will impact the area over which species will be attracted (Langlois et al. 2010).

The mechanistic models outlined by Priede et al. (1990) to estimate the abundance of deep-sea demersal fish from first arrival times are deterministic. However, the arrival rate of fish is stochastically related to population abundance (Farnsworth et al. 2007) and the factors governing aspects of shallow water fish movement are often assumed to be well represented by random distribution. This means it is important to include stochastic elements to mechanistic models. The physical factors, current distribution and velocity, observed around the camera system also have a random distribution within a particular range. Therefore it is important to introduce this random aspect into models to describe fish attraction and arrival at a BUC system. Stochastic models that incorporate both the predictable and random aspects of a process, are increasingly being used to build our understanding of complex natural ecosystems (Brown and Kulasiri 1996). Uses have included stochastic modelling of food web dynamics (Livi et al. 2011) and larval connectivity (Siegel et al. 2008). Farnsworth et al. (2007) also modelled the

arrival process of deep-sea demersal scavengers at the BUC using the addition of stochastic elements to deterministic models.

5.2.5. Simulations

Computer simulations represent an effective way to model the behaviour and movements of biological populations and also to test assumptions and theories regarding the factors influencing movement and behaviours against reality (Huth and Wissel 1992). Simulations have been used to model the swimming behaviours of fish. For example, Huth and Wissel (1992), developed several models to describe the movement of individual fish within a school which they tested using computer simulations and found that models where fish are influenced by all their neighbours described the movement of real schools most accurately. Simulations have also been used to describe larger scale movements of fish, for example to predict the movements of demersal fish stocks on the European Continental Shelf by combining information on fish behaviour and tidal stream data (Arnold and Holford 1995). However, the use of simulations in relation to fish movements around BUC systems has been limited. A simulation was however developed to model the Antarctic fish (*Trematomus bernacchii*) detecting and approaching an artificial bait plume over a few meters. These were built around a number of behavioural parameters that depicted different search strategies and determined that both chemosensory and rheosensory aspects of *T. bernacchii*'s behaviours had to be incorporated into models to match theoretical and in-situ observations of arrival (Montgomery et al. 1999). A number of simulation models have been developed based on correlated random walks of insects attracted to baited pheromone traps (Byers 2007). Trapping programmes lure males of pest species into traps using pheromone components and models have been used to understand the variables affecting insect trapping and the where traps would be most effectively placed (Byers 1993, Byers 2007). Studies to investigate the impact of odour plume dispersal and chemoreceptive abilities on the arrival of crustaceans at traps have also been developed (Watson et al. 2009b). Simulation models have also been used by Addison and Bell, (1997) to improve the understanding of how lobster traps function and have been used to estimate population abundance (Bell et al. 2001, Addison and Bell, 1997).

5.3. Objectives and Hypotheses

5.3.1. Objective 1

The primary objective of this work was to develop a stochastic modelling approach to enable the estimation of absolute abundance of fish and invertebrates using arrival data collected using a shallow water BUC system. This involved the development of species-specific models for six fish and invertebrate species observed in temperate, tropical and Antarctic BUC surveys. A global sensitivity analysis was used to determine the impact of model parameters on the arrival pattern produced by the model.

5.3.2. Objective 2

A secondary objective, following the development of an effective modelling methodology, was to demonstrate how absolute abundance estimates can be generated from BUC data using the modelling methodology. The achievement of this objective was measured by comparing the model absolute abundance outputs to those from corresponding underwater visual census (UVC) transects.

It was hypothesised that:

- 1) The sensitivity analysis would show which model variables have an effect upon the arrival pattern of fish or invertebrates at the BUC and what aspects of the arrival pattern variable affect the most (i.e. Max_N , t_{arrival} and t_{maxN})
- 2) The modelling methodology would generate absolute abundance estimate that were comparable to those from corresponding UVC surveys.

5.4. Materials and Methods

5.4.1. General Model Outline

The simulation was built in MATLAB (R2010b) using the movement of an individual fish around a BUC system within a designated area. A bait plume was plotted and the area

covered (B_a , m²) was described as a sector of a circle, using the 3 equations below. The length of the plume (L_{pl} , m) was calculated using a radius described as the mean current speed (V_w , ms⁻¹) recorded throughout the deployment multiplied by the simulation time (T , seconds). The plume therefore expanded with every time step of the simulation. The plume angle (Pl_θ , radians) was calculated from the inverse tangent of the diffusional velocity (B_y , ms⁻¹), divided by the current speed (V_w , ms⁻¹). The relationship between these model parameters is described in the equations:

$$L_{pl} = V_w T$$

$$Pl_\theta = 2 \tan^{-1} \left(\frac{B_y}{V_w} \right)$$

$$B_a = \left(\frac{\theta}{2} \right) L_{pl}^2$$

Simulations depict the movement of a population of a fixed abundance within a defined area (A , m²). Prior to detection of the bait plume fish move at a cruising speed (V_{cr} , ms⁻¹) or are stationary, and turned a random number of times (T_r) within a set time period known as the turning interval (Int_{tr} , seconds). The direction within which the fish travels after each turn (D_r , radians) was randomly selected (independently for each individual).

$$D_r = rand(0, 360)$$

$$Int_{tr} = rand(0, T_r) * T_r$$

The starting point ($P_{st}, (x, y)$) was selected (again independently for each individual) from a random position within the simulation area (A , m²) using the formula below:

$$(P_{st}, (x, y)) = rand \left(-\frac{A}{2}, \frac{A}{2} \right)$$

The distance travelled per time step (D_s , m) was calculated by dividing the cruising speed by the time resolution (T_r , seconds). Distance travelled in the x and y axis ($D_s(x, y)$) was found by multiplying the cruise speed divided by the simulation time resolution (length of the time-step used in simulations) and multiplying this by sine and cosine of the direction (D_r , radians):

$$D_s(x) = \frac{V_{cr}}{T_r} \sin(D_r)$$

$$D_s(y) = \frac{V_{cr}}{T_r} \cos(D_r)$$

The distance to the camera ($D_{cm}(x, y)$) was calculated by taking the square root of the distance travelled in the x and y axis:

$$D_{cm}(x, y) = \sqrt{D_s(x, y)^2}$$

When the distance to the camera ($D_{cm}(x, y)$) is less than the radius associated with the circular bait area (B_a, m^2) the fish is considered to have encounter the bait plume area. On encounter the fish turns into an approach angle $app(\theta)$ calculated using:

$$app(\theta) = (180, 360, 0, -180 \tan^{-1} D_s\left(\frac{x}{y}\right))$$

(the angle used in this equation depends upon the position on the fish when the bait plume is encountered). This change in direction causes the fish to swim directly upstream towards the bait at a through-water approach speed up the plume towards the camera ($V_{f sa}, ms^{-1}$). This speed is faster than the cruising swimming speed and was calculated from observation of fish max swimming speed in previous published studies. Current speed (V_w, ms^{-1}) is subtracted to account for the fish swimming upstream against the current. Once in the bait plume the distance travelled towards the camera and its relation to the camera position is recalculated using the through-water approach speed ($V_{f sa}, ms^{-1}$):

$$D_s(x) = \frac{V_{f sa}}{T_r} \sin(D_r)$$

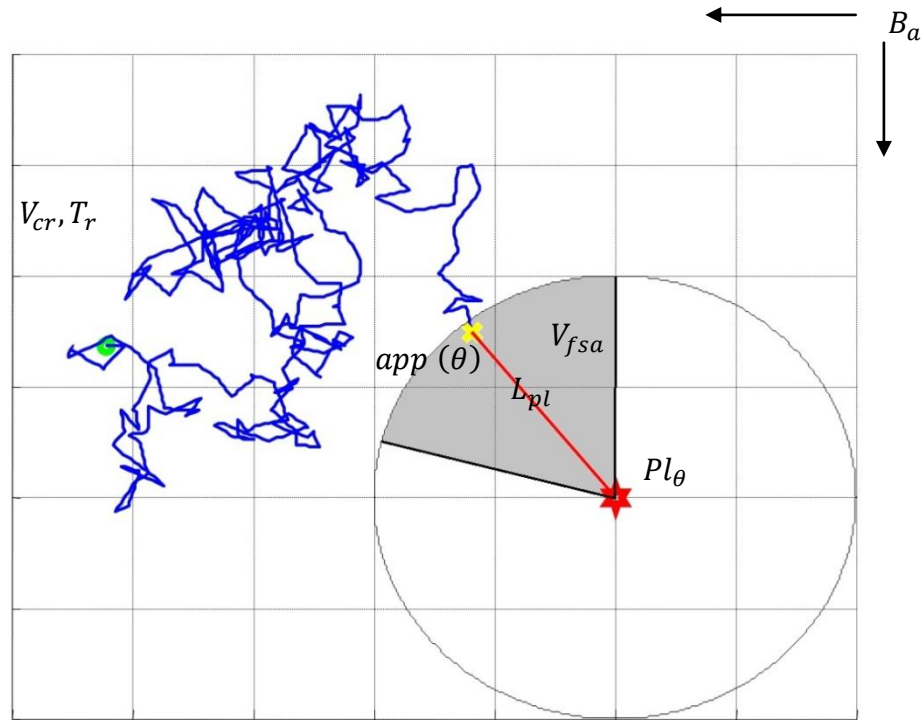
$$D_s(y) = \frac{V_{f sa}}{T_r} \cos(D_r)$$

Upon reaching the bait the individual will remain there for a “staying time” (S_t , seconds) found by taking a random time between a pre-determined interval. This was multiplied by the time resolution (T_r , seconds) of the simulation:

$$S_t = rand([1800, T_r])$$

After remaining at the camera for the staying time the fish is removed from the simulation as it is assumed to have reached satiation or decided to forage elsewhere. Simulations run for 60 or 90 minutes and record the total number of fish, or invertebrates, present at the bait every 30 seconds, the same interval is used in the in-situ BUC studies. The model is depicted in as a diagram in Fig. 5.1.

Figure 5.1. Diagram illustrating the general input and output parameters of the model simulation describing the behaviour of fish and invertebrate populations in relation to a baited underwater camera system.



5.4.2. General Assumptions

Fish are assumed to act independently of each other at all stages of the simulation and to always react to the bait plume on encounter. The bait plume was always spread from the origin of the coordinate system used in the simulations and assumed that the bait plume dispersed in a single direction. The models currently do not account for the dilution of the bait plume with time and distance from the bait and also potential changes in current direction commonly observed in the shallow water environment. The current model therefore assumes a constant plume concentration. However, the models presented are a framework that will be combined with fluid dynamics models of bait plume dispersal from a point source recently developed at Ocean Lab, University of Aberdeen, in collaboration with Dr Alan Jamieson. This will enable the dilution of the plume concentration and changes in current direction to be incorporated into the models.

5.4.3. Species Specific Models

Simulations were developed for six species; the temperate fish saithe (*Pollachius virens*) and the lesser spotted dogfish (*Scyliorhinus canicula*) both recorded in BUC deployments on the West coast of Scotland (Chapter 2), the grouper *Epinephelus fasciatus* and moray eels of the genus *Gymnothorax spp.* recorded in BUC deployments in the tropical Gulf of Aqaba (Chapter 3) and the Antarctic scavenging invertebrates *Odontaster validus* and *Parbolasia corrugatus* (Chapter 4). Data on swimming speeds, the turning frequency and aspects of the foraging behaviours for each species were determined from published studies. Estimations of staying time were based on observation of individuals in BUC deployments. For many of the species observed it was difficult to identify individuals to calculate their staying time at the bait and estimations were taken from observation of the number of consecutive images an individual of that species was observed in. However, for *S. canicula* it was possible to identify individuals with specific markings which enabled them to be recognised throughout the deployments allowing staying times to be estimated. Current velocity was recorded during deployments using a current meter and provided the current ranges within which the simulation could operate. The ranges of input parameters for each model are described in Table 5.1 and current meter data is displayed in Fig. 5.2 (a - c).

Table 5.1. Input parameters ranges for *Epinephelus fasciatus*, *Gymnothorax spp*, *Pollachius virens*, *Scyliorhinus canicula*, *Odontaster validus* and *Parbolasia corrugatus*.

Parameters	Area (m ²)	Current speed (m s ⁻¹)	Abundance (individuals)	Cruising speed (m s ⁻¹)	Turning interval (s)	Approach speed (m s ⁻¹)	Staying time (s)
Species							
<i>Pollachius virens</i>	1000	0.01 – 0.25	1 - 100	0 – 0.5	0 – 120	0.4 – 1.2	0 – 360
<i>Scyliorhinus canicula</i>	1000	0.01 – 0.25	1 - 100	0	0 - 120	0.2 – 0.65	0 - 360
<i>Epinephelus fasciatus</i>	1000	0.02 – 0.2	1 - 100	0	0 – 120	0.294 – 0.365	0 - 240
<i>Gymnothorax spp.</i>	1000	0.02 – 0.2	1 - 100	0	0 – 120	0.0935 – 0.318	0 – 180
<i>Odontaster validus</i>	6.25	0.01 – 0.1	1 - 100	0	n/a	0.0001 – 0.001	To simulation end
<i>Parbolasia corrugatus</i>	6.25	0.01 – 0.1	1 - 100	0	n/a	0.0001 – 0.0003	To simulation end

5.4.4. Temperate Baited Underwater Camera Models

See Chapter 2 for details on the BUC deployment methods used to gather data for the development of these models. The diffusional velocity used for temperate models for *P. virens* and *S. canicula* was taken from values gathered from dye tracing experiments on the West coast of Scotland, estimates to range between 0.01 and 0.1 ms⁻¹ (Riddle and Lewis 2000). The current velocities used in the temperate models ranged between 0.01 and 0.25 ms⁻¹ from examination of the current speeds observed during BUC deployments on the West coast of Scotland (Fig. 5.2a).

5.4.4.1. *Saithe (Pollachius virens)*

The cruising swimming speed of *P. virens* has been recorded in a number of studies (Johnston and Moon 1980, Videler and Hess 1984, Steinhausen et al. 2005). Swimming speeds from publications were recorded in body lengths s⁻¹ and this was converted to m s⁻¹ using the size range of fish observed at the bait of the camera. Measurements were made using Image Pro Plus[®] using the bait bag for calibration. The approach velocity towards the bait was determined from estimates of the maximum swimming speed of *P. virens* in publications (Blaxter and Dickson 1959, Videler and Hess 1984, He and Wardle 1988).

Individuals swam at a cruising speed between 0 - 0.5 m s⁻¹ and turned a random number of times every 0 - 120 seconds. On contact with the bait they swam at an approach velocity of 0.4 - 1.2 m s⁻¹ toward the bait. On reaching the bait individuals remained there for a period of time randomly selected between 0 - 360 seconds. The model simulates 100 fish moving within a 1000 m² square area with the BUC at the centre.

5.4.4.2. *Lesser Spotted Dogfish (Scyliorhinus canicula)*

The lesser spotted dogfish (*S. canicula*) was the most commonly observed species in BUC deployments on the West coast of Scotland. Even though this is an abundant species around European waters and an important species for physiological experiments, limited research has examined their *in situ* movements (Sims et al. 2001). However, tracking studies have found that there is a sexual segregation in foraging patterns, even though both sexes generally will be stationary before coming in contact with a bait either inside a

refuge or on the seabed (Sims et al. 2001). The cruising speed of *S. canicula* in models was therefore set to zero and individuals only moved once in contact with the bait plume. The approach speed of *S. canicula* was taken from the maximum swimming speeds from studies of the closely related species, *Squalus acanthius* and *Scyliorhinus stellaris*, that inhabit a similar habitat to *S. canicula* (Curtin and Woledge 1988). Approach speeds ranged between $0.2 - 0.65 \text{ m s}^{-1}$ (Alexander 1981, Anderson et al. 2001). On reaching the bait individuals remained there for a period of time randomly selected between $0 - 360 \text{ s}$. The model simulates 100 *S. canicula* moving within a 1000 m^2 area.

5.4.5. Tropical Baited Underwater Camera Models

The BUC deployment methods used to gather data for the development of these models are described in Chapter 3. The diffusional velocity was estimated at 10^{-3} m s^{-1} in the deep sea environment according to the models of scavenger arrival at a baited camera by Sainte-Maire and Hargrave, (1987) was used in models for the tropical reef fish (*Gymnothorax spp.* and *E. fasciatus*). For both tropical species the range of current speeds used in simulations were taken from RDI Sentinel ACDP readings made during BUC deployment from the Interuniversity Institute for Marine Sciences, Eilat, pier. The currents speeds observed during the BUC deployments in the Gulf of Aqaba ranged between 0.02 and 0.2 m s^{-1} (Fig. 5.2b). Current speeds were approximately comparable to the current speeds measured in the deep sea environment by Sainte-Maire and Hargrave, (1987), which ranged between 0.008 and 0.07 m s^{-1} . Therefore, due to the lack of measurements of the diffusional velocities in the tropical environment the same diffusional velocity was used in tropical models.

5.4.5.1. *Black Tip Grouper (Epinephelus fasciatus)*

Many groupers of the family Serranidae have been described as displaying territorial and stationary behaviour prior to ambushing prey and to forage within a limited area of the reef (Diamant and Shpigel 1985), e.g. the dusky grouper (*Mycteroperca marginata*) (Condini et al. 2011) and the red grouper (Farmer and Ault 2011). Blacktip groupers (*Ephinephelus fasciatus*) are ambush predators highly associated with rocky reefs and crevices and will defend a small territory (Gibran 2007). Therefore in simulations of *E. fasciatus* movement around the BUC system individuals remained stationary prior to the detection of the bait

plume. On contacting the plume they swam towards the source at an approach speed between 0.294 and 0.365 m s⁻¹. This estimate was derived from raw data from a study of another Serranid, *Cephalopholis boenak*, provided by Dr C. Fulton and published in (Fulton 2007). Staying times were randomly selected between 0 – 240 seconds and 1 to 100 individuals were modelled over a 1000 m² square area. Current speeds ranged between 0.02 and 0.2 m s⁻¹ which corresponded to the range of speeds recorded in the *in situ* deployments (Fig. 5.2b).

5.4.5.2. Moray Eel (*Gymnothorax* sp).

Moray eels of the genus *Gymnothorax* are nocturnal ambush predators and primarily remain within a rocky reef refuge during the day (Diamant and Shpigel 1985, Bshary et al. 2006). Therefore in simulations they were modelled as stationary prior to the detection of the bait plume but on contact moved towards the source at a velocity of 0.0935 to 0.318 ms⁻¹ in accordance to the sprint swimming speeds recorded for the European eel (*Anguilla anguilla*). *A. anguilla* swimming speeds were used as data on the swimming speed of moray eels is limited and both *A. anguilla* and moray eels perform anguilliform swimming motions (Blaxter 1969, D'Aout and Aerts 1999). On reaching the bait individuals remained there for a period of time randomly selected between 0 - 180 seconds. 100 individuals were modelled over a 1000 m² area.

5.4.6. Antarctic Baited Underwater Camera Models

See Chapter 4 for details on the BUC deployment methods used to gather data for the development of these models. Antarctic invertebrate scavengers are slow moving compared to the temperate and tropical fish therefore BUC deployments in the shallow water Antarctic environment lasted for 1.5 h. The invertebrates also crawl along the seabed so current velocity was not subtracted from the approach velocity. The diffusional velocity estimated at 10⁻³ m s⁻¹ for the deep sea environment according to the models of scavenger arrival at a baited camera by Sainte-Maire and Hargrave, (1987) was used in models for the Antarctic scavenging invertebrates *Odontaster validus* and *Parbolasia corrugatus*. The currents speeds observed during the deployments in the Western Antarctic Peninsula ranged between 0.01 and 0.1 m s⁻¹ (Fig 5.2c). Current speeds were comparable to the deep sea currents described in Sainte-Marie and Hargrave, (1987).

5.4.6.1. Asteroid (*Odonaster validus*)

The Antarctic asteroid *O. validus* is an omnivorous predator and scavenger and has been previously shown to respond to chemical cues to locate food (Kidawa 2005, Kidawa et al. 2010). Previous studies have also found that this species is commonly caught in baited traps and was regularly observed in the BUC deployment described in Chapter 4.

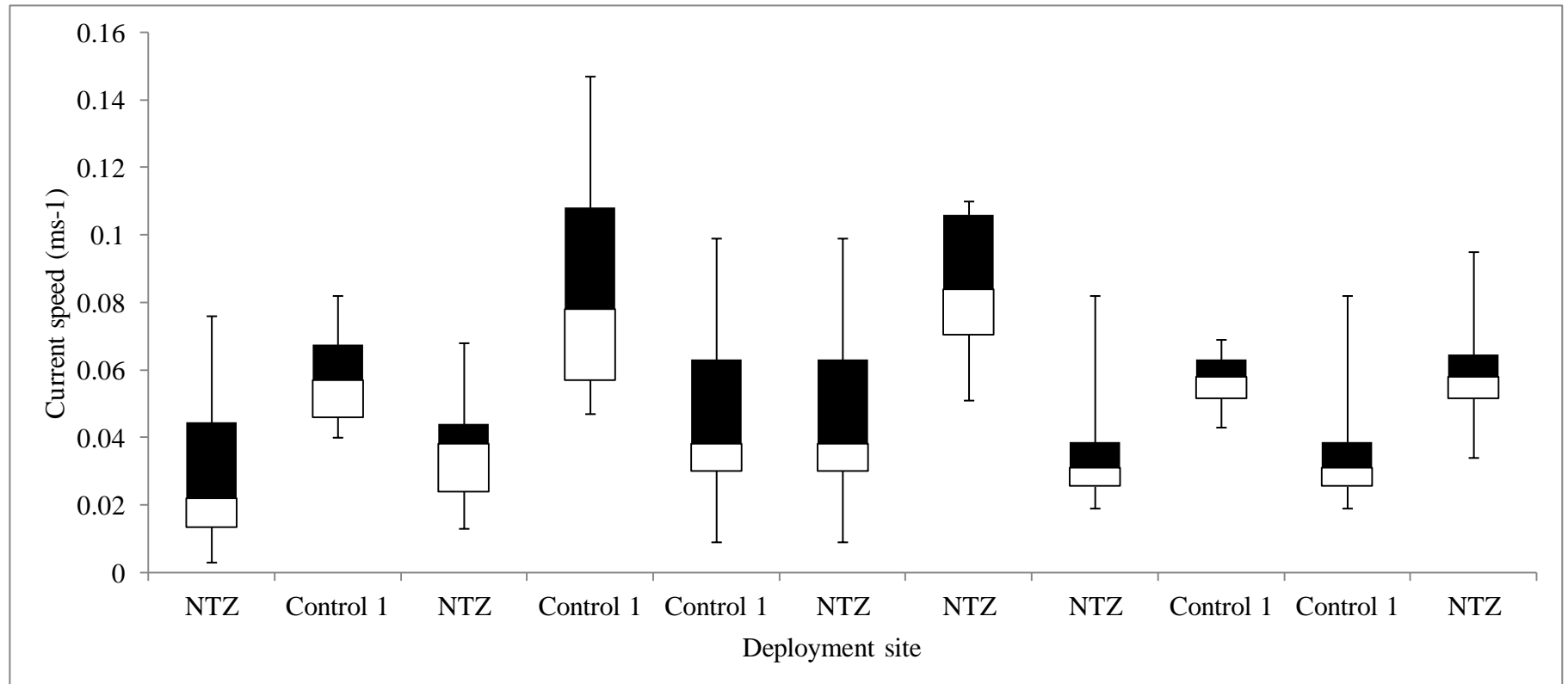
O. validus abundances ranged between 0 and 100 individuals and were modelled over a 6.25 m² area. *O. validus* remains relatively stationary prior to the detection of an odour plume and moved at a speed between 0.0001 and 0.001 m s⁻¹ towards the bait. Approach speeds of *O. validus* were recorded from time-lapse images from BUC deployments. This was possible as individuals approaching the bait could be identified throughout the deployment due to their slow movement speeds, compared to the movements of mobile fish species modelled in the temperate and tropical environments. This speed range matches that observed in McClintock et al. (2008) and Kidawa et al. (2010) aquarium study of the approach of *O. validus* towards a bait. On reaching the bait *O. validus* remained there till the end of the simulation as observed in BUC deployments.

5.4.6.2. Nemertean Worm (*Parbolasia corrugatus*)

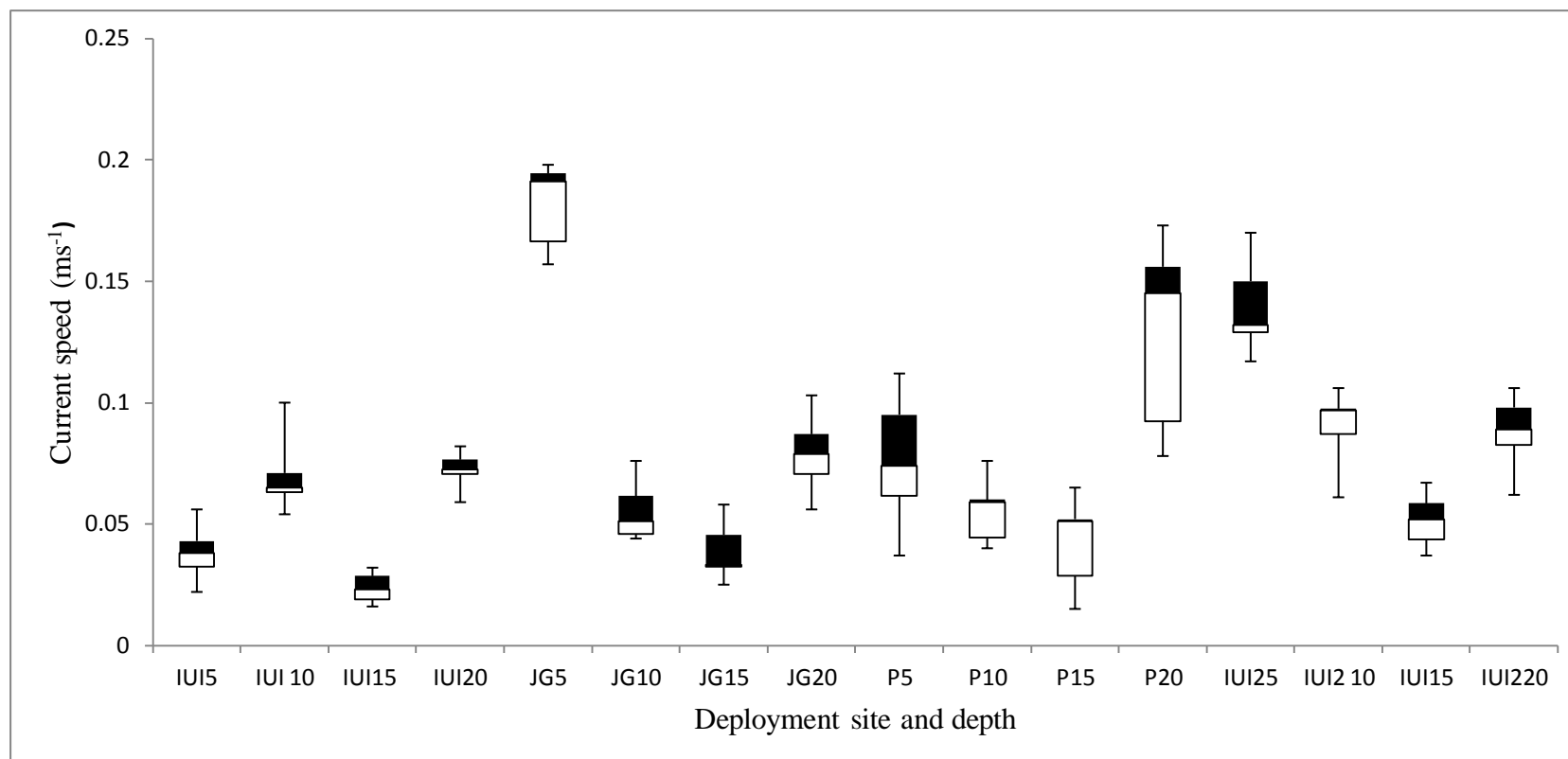
P. corrugatus abundances ranged between 0 and 100 individuals and were modelled over a 6.25 m² area. The nemertean worm *P. corrugatus* is an abundant predator and scavenger in shallow subtidal Antarctic waters which will consume a wide range of prey. Large congregations will migrate to and feed upon the carcasses (Clarke and Prothero-Thomas 1997, Ericson et al. 2010). *P. corrugatus* is active in low light levels and during the day will spend the majority of its time under rocky refugia (Clarke and Prothero-Thomas 1997). However, they do appear to leave their refugia when an odour plume is detected (personal observation). In models *P. corrugatus* were therefore assumed to be stationary prior to the detection of an odour plume and moved at an approach velocity of 0.0001 – 0.0003 m s⁻¹ towards the bait. The approach speed was measured in BUC deployments time lapse images. The model assumed that on reaching the bait they remained there till the end of the simulation as was observed in BUC deployments.

Figure 5.2 a – c. Box plots of mean (\pm SE) showing distribution of current meter data from a) temperate, b) tropical and c) Antarctic BUC deployments.

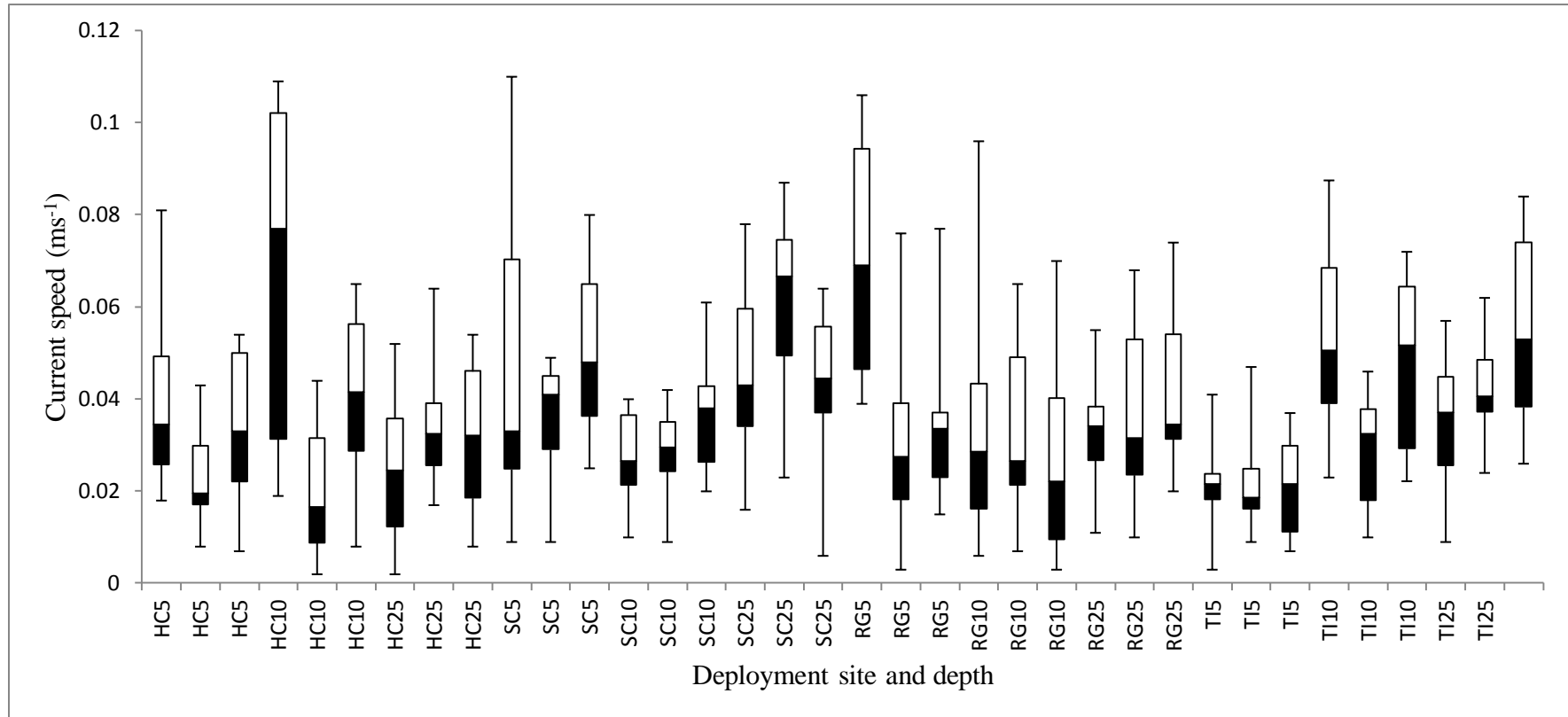
a)



b)



c)



5.4.7. Data Analysis

Models generated an arrival patterns of fish and invertebrates at the bait every 30 seconds, to produce a dataset in the same form as that from *in situ* BUC deployments. From this the maximum number of fish or invertebrates at the bait at one time (Max_N) and the time to arrival of the first individual of each species ($t_{arrival}$) and the time to reach Max_N (t_{maxN}) were used to describe the arrival pattern.

5.4.7.1. *Sensitivity Analysis*

Sensitivity analysis enables the dependence of the fish or invertebrate arrival pattern output by the model on input parameters to be determined and was used to test hypothesis one. A global approach analyses the impact of the full set of parameters and is most suitable for systems with non-linear dynamics such as those generally observed in dynamic biological systems that incorporate a complex network of parameters (Kiparissides et al. 2009). A global sensitivity analysis was performed on each species-specific model to determine the impact of the input variables; population abundance, current speed, diffusional velocity, swimming speed before contact with the odour plume, approach speed and staying time. Each input parameter was set to be randomly selected from the full range of potential values and each of the six models was run 300 times to ensure that the full range of potential input parameters was considered. This was checked by plotting a histogram of the distribution of the input parameters and was also used to ensure that the range of input values had a random distribution (Fig. 5.2). Both the marginal and bivariate simulated factor distributions were explored to ensure that coverage of the factor space was extensive.

A stepwise regression was performed in R to examine the relationship between the input variables and the model output abundance indices; Max_N , $t_{arrival}$ and t_{maxN} . The relationship between any input variable identified as having a significant effect on Max_N , $t_{arrival}$ and t_{maxN} was plotted in a scatter plot (Fig 5.5 - 5.10). The relationship between the model variables and the BUC abundance indices were unknown as this early stage of model development and the stepwise regression was used as a tool to explore these relationships.

The analysis of the influence of model parameters on the resultant fish or invertebrate arrival pattern highlighted which parameters were important to calibrate with *in situ* measurements. Any abundance indices which reflected a significant proportion of the input population abundance would be used to match individual arrival patterns at the BUC model with that of the BUC in-situ observation to generate an absolute abundance estimate.

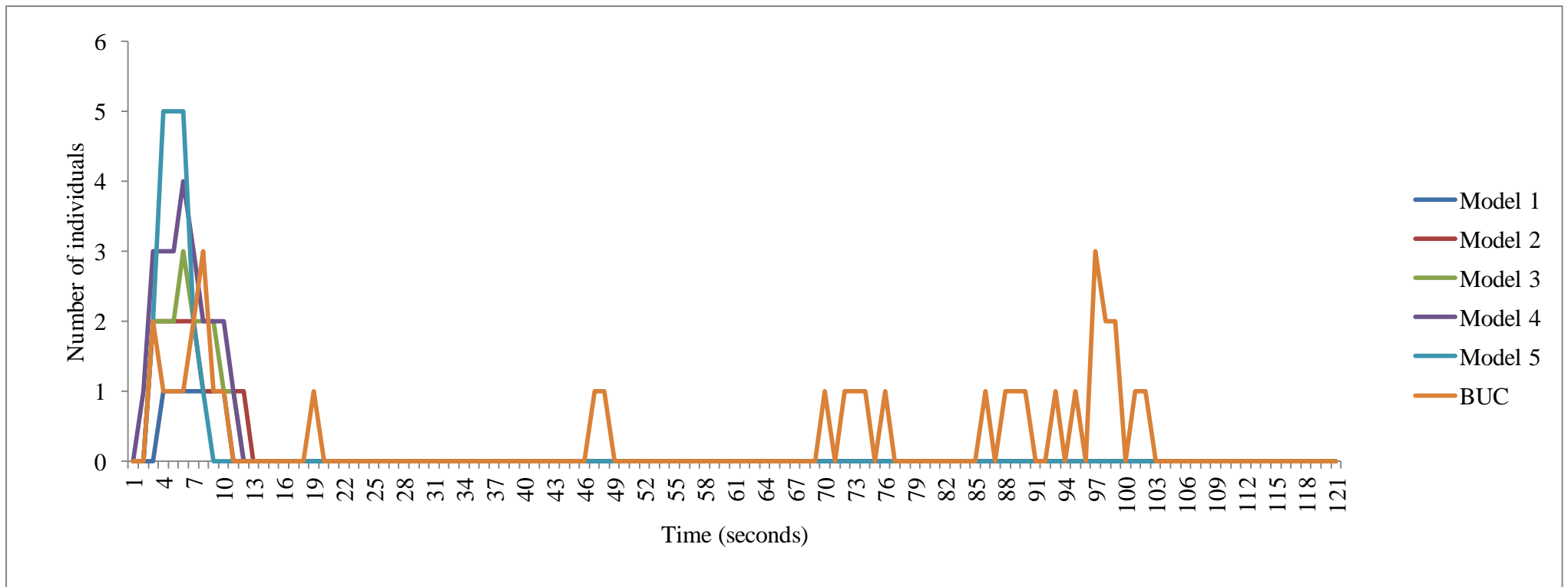
5.4.7.2. *Producing Absolute Abundance Estimates from BUC Data*

First the model was calibrated for any input parameter with a significant impact on the model arrival pattern, measured by examining the effect of parameters on the Max_N , $t_{arrival}$ and t_{maxN} produced by models in the sensitivity analysis. Any parameters with a significant effect were parameterised using an in-situ measurement of this variable where available. For example, if current speed had a significant impact on the Max_N then the current speed from the in-situ BUC deployment being used to produce an abundance estimate was used as a model input. Those identified as having no significant impact on the model output were set to be selected randomly from a range of suitable values for that measure. However, for some parameters an in-situ measurement was not available and values within the models had to remain as the estimates ranges. These parameters could be however, highlighted as those requiring measurement to improve the model.

To produce absolute abundance estimates using the modelling methodology a suitable range of estimated population abundances must be first input into the model. In practice these estimates could be derived from other survey methods, for example underwater visual transects (UVCs) or trawl surveys, or be a best guess at the highest and lowest possible abundances for the focal species. Corresponding UVC surveys from the same position and approximately the same time as the BUC deployments made in the Gulf of Aqaba and Antarctica, described in Chapter 3 and 4, were used to find a suitable abundance range for the tropical and Antarctic models. Each single population abundance input into the model produced a BUC arrival pattern. For example, if an abundance range of 1 – 100 individuals was used 99 arrival patterns would be produced. These arrival patterns are compared to those from the corresponding BUC survey. Any of the three arrival pattern indices (Max_N , $t_{arrival}$ or t_{maxN}) found to be significantly related to model input abundance in the sensitivity analysis were used to describe the arrival patterns from

the model and the in-situ BUC. The abundance index or indices were used to find a match between the multiple model arrival patterns and that from the corresponding *in situ* BUC deployment. Once a match was found the population abundance input into the model to produce that arrival pattern is recorded as the model's best estimate of the absolute abundance of the fish or invertebrate population surveyed by the BUC system. This process is illustrated in Fig. 5.3 where the arrival pattern from five model runs of the model of *E. fasciatus* movement around the BUC can be compared to that of the in-situ BUC arrival pattern. The Max_N of the arrival pattern from the *in situ* BUC can be compared to determine the best match from arrival patterns of the five models. The model with the Max_N nearest to the *in situ* Max_N was selected as the model with the arrival pattern that best matched that from the *in situ* BUC. From this plot it can be seen that the Max_N of the BUC arrival pattern matches best with model three. The population abundance input into model three would therefore be the BUC model abundance estimate.

Figure 5.3. Example plot of the arrival pattern of the black tip grouper (*Epinephelus fasciatus*) at the baited underwater camera system (BUC) produced by 5 model runs and the arrival pattern from an *in situ* BUC deployment.



5.4.7.3. Comparison to In Situ Baited Underwater Camera Data

The absolute abundance estimate produced using the model methodology and BUC data were compared to those generated by corresponding UVC surveys to validate the ability of the model to produce accurate abundance estimates. Models describing the movement of the two tropical fish species (*E. fasciatus* and *Gymnothorax spp.*) and the two Antarctic invertebrate scavengers (*O. validus* and *P. corrugatus*) in relation to the BUC system were validated using transect data collected at the same position and approximately the same time. Transect data that corresponded to temperate BUC deployments was however, not available so a comparison could not be made. For each of the 16 BUC deployments from the Gulf of Aqaba and the 18 from one site, South Cove, in Ryder Bay, West Antarctic Peninsula the procedure detailed in 5.3.7.1 was performed and the resultant model absolute abundance estimates were compared to those from the corresponding UVC surveys using a Bland –Altman analysis (Bland and Altman 1986). The measurements of absolute abundance produced by both methods were also displayed in histograms and scatter plots (Fig. 5.11 a – d).

A Bland and Altman analysis is used to compare two methods of measurement, usually a new method with an established one (Bland and Altman 1986). In this study the UVC represents the established method for measuring fish and invertebrate absolute abundance and the BUC the new method. Usually in this form of analysis the true measurement is unknown, as is true when measuring the abundance of these marine populations. The Bland and Altman method graphical plots the mean difference between the two corresponding measurements from both methods, known as ‘the bias’, and the 95% limits of agreement as $\pm 1.95SD$ of the mean difference. The plot enables visual judgement of the agreement between the measurements and the smaller the range between the measurements the better the match (Bland and Altman 1986, 1995). An analysis showing no significant systematic bias between the two methods would show the majority of the data points within the confidence limits and that points would have a symmetrical around zero. The Bland and Altman analysis method is most commonly used in medical research and ultimately aims to determine whether the methods can be used together or whether the new method can be used to replace the established one (Myles and Cui 2007). A Bland and Altman analysis was performed in the R package ‘MethComp’ and a Bland-Altman plot and measures of the test bias test were produced to compare the measurements of absolute abundance using the UVC and tropical (*E. fasciatus* and *Gymnothorax spp.*) and

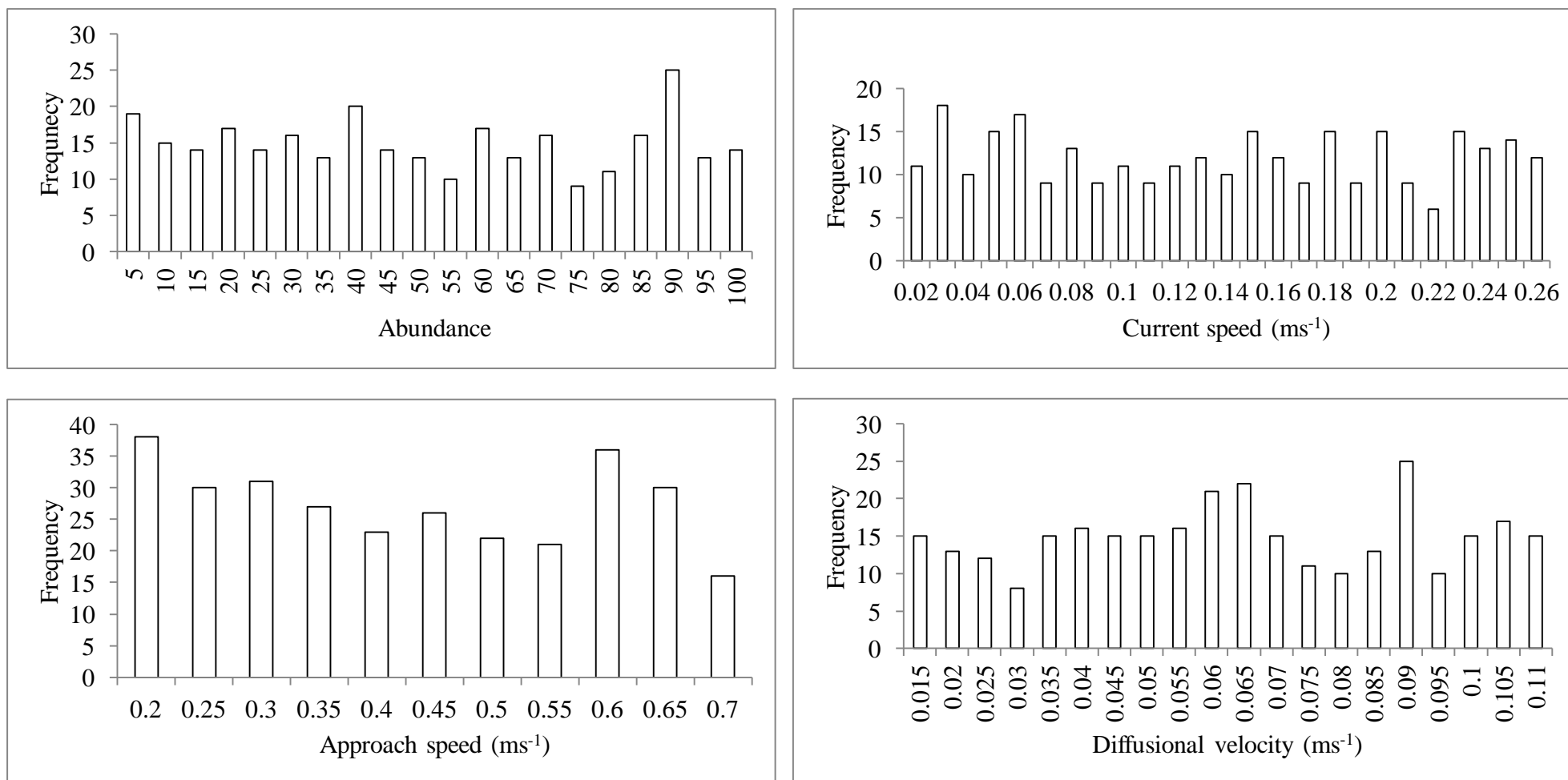
Antarctic (*O. validus* and *P. corrugatus*) BUC models (Fig. 5.12 a – d). This analysis enabled hypothesis 2 to be tested.

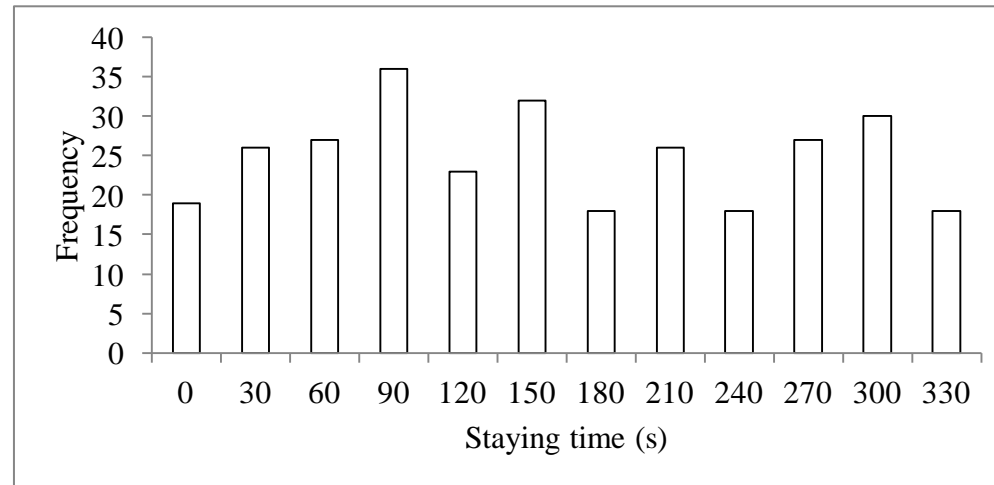
5.5. Results

5.5.1. Global Sensitivity Analysis

The input parameters (abundance, current speed, approach speed, cruising speed, diffusional velocity and staying time) produced by 300 runs of the 6 models were plotted in frequency histograms and found to consider the full range of parameters. An example plot for *S. canicula* is displayed in Fig. 5.4.

Figure. 5.4. Histograms of the distribution of the model input variables; abundance , current speed (m s^{-1}), approach speed (m s^{-1}), diffusional velocity (m s^{-1}) and staying time (s) for *Scyliorhinus canicula*





Sensitivity analysis revealed that the model input parameters explained a large proportion of the variability in the Max_N out of the 6 models. Input parameters explained less of the variability in the time based metrics (t_{arrival} and t_{maxN}). Input abundance was the model parameter that had the greatest impact on the Max_N, t_{arrival} and t_{maxN} outputs from the model for all 6 species.

In temperate models of *P. virens* movement in relation to the BUC system, the input parameters accounted for 98.06% ($P < 0.0001$) of the variability in Max_N, 45.91% ($P < 0.0001$) in t_{arrival} and 51.39% ($P < 0.0001$) in t_{maxN} . Input parameters accounted for 88.94% of the variability in Max_N, 23.89% in t_{arrival} and 24.41% in t_{maxN} for models of *S. canicula*.

Population abundance accounted for 97.6% and 81.64% of the variability in the Max_N output ($P < 0.0001$ and $P < 0.0001$) for models of *P. virens* and *S. canicula*. Approach speed had a much smaller but significant effect upon both *P. virens* and *S. canicula* Max_N (R-sq (adj) = 1.46% and 7.84%, $P = 0.02$ and $P < 0.05$). Input parameters explained less of the variability in t_{arrival} values generated by both *P. virens* and *S. canicula* models however, again the most significant regressions were with fish abundance (R-sq (adj) = 21.58% and 9.11%, $P < 0.0001$ and $P < 0.0001$). The approach speed of both temperate species also had a significant effect on the values of t_{arrival} generated (R-sq (adj) = 26.8% and 7.82%, $P < 0.0001$ and $P < 0.0001$). Current speed also had a significant effect upon *S. canicula* t_{arrival} (R-sq(adj) = 3.85, $P = 0.0004$). Population abundance however, had no impact on t_{maxN} values for *S. canicula*, which was significantly affected by fish approach velocity (R-sq (adj) = 32.7% , $P < 0.0001$) and current velocity (R-sq (adj) = 4.50%, $P < 0.0001$). Population abundance did have a significant effect on *P. virens* t_{maxN} (R-sq (adj) = 22.2% , $P = 0.0006$) as did approach speed (R-sq (adj) = 46.8% , $P < 0.0001$).

Diffusional velocity, cruising speed or staying time had no significant impact on any of the abundance metrics recorded for the temperate fish species. Detailed stepwise regression results are displayed in detail in Table 5.2. Scatter plots of the relationships between significant input variables and Max_N, t_{arrival} and t_{maxN} from the temperate models are displayed in Fig 5.5. and 5.6. Examination of some of the scatter plots shows that a linear relationship is not present between some of the parameters which the sensitivity analysis deemed to be significant. These regressions had significant p-value but low R-squared values however, the p-value are potentially influenced by the sample size. The relationship

between these parameters and the abundance indices are not considered significant in further analysis.

For both tropical models the parameter population abundance explained a large proportion of the variability in the Max_N output; 91.74% for *E. Fasciatus* and 97.99% for *Gymnothorax spp.* ($P < 0.0001$ and $P < 0.0001$). As in the temperate models, input parameters explained less of the variability in the t_{arrival} of tropical fish at the bait. Population abundance had a small but significant effect on *E. fasciatus* ($R\text{-sq (adj)} = 18.16\%$, $P < 0.0001$) and *Gymnothorax spp.* t_{arrival} ($R\text{-sq (adj)} = 30.17\%$, $P < 0.0001$). Current speed also had a significant impact on *Gymnothorax spp.* t_{arrival} ($R\text{-sq (adj)} = 1.47\%$, $P = 0.02$). Current speed had a greater impact on the t_{maxN} output for both tropical species than observed for temperate species respectively and explained 1.8% of the *Gymnothorax spp.* t_{maxN} ($P = 0.018$). Population abundance had a small but significant impact on *E. fasciatus* t_{maxN} ($R\text{-sq (adj)} = 6.71\%$, $P < 0.0001$). As in the temperate models staying time had no effect upon indices for both tropical models. Detailed stepwise regression results are displayed in detail in Table 5.2. Scatter plots of the relationships between significant input variables and Max_N , t_{arrival} and t_{maxN} from the tropical models are displayed in Fig 5.7. and 5.8. Scatter plots of the relationship between t_{arrival} and t_{maxN} and current speed for *E. fasciatus* did not show evidence of a linear regression, either did t_{arrival} and t_{maxN} and abundance for *Gymnothorax spp.*

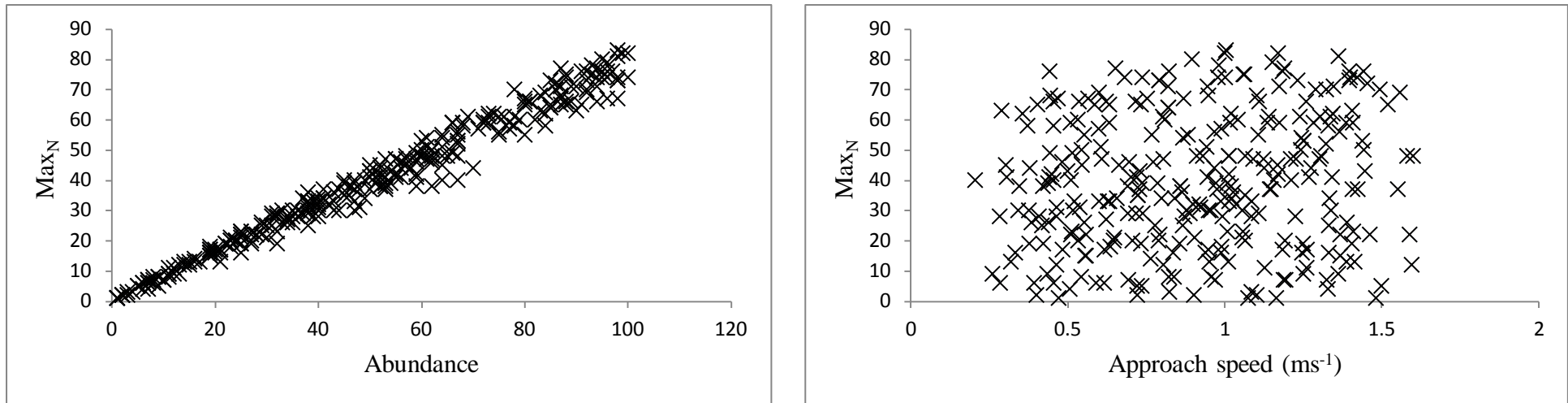
Only population abundance input into models of the Antarctic asteroid *O. validus* movement around the BUC also explained a significant proportion of the Max_N values generated ($R\text{-sq (adj)} = 49.32\%$) ($P < 0.0001$). *O. validus* t_{arrival} and t_{MaxN} values were also only significantly affected by input abundance ($R\text{-sq (adj)} = 19.14$ and 3.37 , $P < 0.0001$ and $P = 0.0008$). For *P. corrugatus* input abundance accounted for 34.48% of the variability in Max_N ($P < 0.0001$) and t_{arrival} and t_{maxN} 19.29% and 1.49% ($P < 0.0001$ and $P = 0.03$). Current speed and *P. corrugatus* approach speed had no significant effect upon Max_N , t_{arrival} and t_{maxN} values. Detailed stepwise regression results are displayed in detail in Table 5.2. Scatter plots of the relationships between significant input variables and Max_N , t_{arrival} and t_{maxN} from the Antarctic scavenger models are displayed in Fig 5.9. and 5.10. Scatter plots of the relationship between t_{arrival} and t_{maxN} and abundance for *O. validus* and *P. corrugatus* did not show evidence of a linear regression.

Table 5.2. Stepwise regression results of significant relationships between the model inputs parameters; input parameters abundance, cruise velocity (V_{cr}), approach velocity (V_{fsa}), current velocity (V_w), staying time (S_t) and the outputs; Max_N , $t_{arrival}$ and t_{maxN} .

Species	Output Index	Input parameter	SE Coef	T-value	P-value	R-sq(adj)
<i>Pollachius virens</i>	Max_N	Abundance	0.01	110.77	<0.0001	97.60%
		V_{fsa}	3.68	2.33	0.02	1.46%
	$t_{arrival}$	Abundance	0.04	-9.26	<0.0001	21.58%
		V_{fsa}	2.94	-10.48	<0.0001	26.80%
	t_{maxN}	Abundance	0.08	2.79	0.006	2.22%
		V_{fsa}	4.85	-16.24	<0.0001	46.76%
<i>S. canicula</i>	Max_N	Abundance	0.02	36.47	<0.0001	81.64%
		V_{fsa}	6.83	5.14	<0.0001	7.84%
	$t_{arrival}$	Abundance	0.26	-5.57	<0.0001	9.11%
		V_{fsa}	48.88	-5.13	<0.0001	7.82%
		V_w	104.91	3.60	0.0004	3.85%
	t_{maxN}	V_{fsa}	144.95	-6.99	<0.0001	32.7%
		V_w	320.60	3.89	0.0001	4.51%
<i>E. fasciatus</i>	Max_N	Abundance	0.012	57.47	<0.0001	91.70%
	$t_{arrival}$	Abundance	0.059	-8.33	<0.0001	18.16%
	t_{maxN}	Abundance	0.150	4.75	<0.0001	6.71%
<i>Gymnothorax</i>	Max_N	Abundance	0.01	120.63	<0.0001	97.99%
	$t_{arrival}$	Abundance	0.050	-11.41	<0.0001	30.17%

		V _w	29.44	2.33	0.0202	1.47%
	t _{maxN}	V _w	50.56	2.38	0.018	1.80%
<i>O. validus</i>	Max _N	Abundance	0.04	17.09	<0.0001	49.32%
	t _{arrival}	Abundance	2.75	-8.47	<0.0001	19.14%
	t _{maxN}	Abundance	1.72	3.38	0.0008	3.37%
<i>P. corrugatus</i>	Max _N	Abundance	0.02	11.14	<0.0001	34.48%
	t _{arrival}	Abundance	3.49	-7.55	<0.0001	19.29%
	t _{maxN}	Abundance	2.36	2.13	0.034	1.49%

Figure 5.5. Scatter plots of the significant regression relationships between Max_N , t_{arrival} and t_{maxN} and input parameters abundance and approach speed (V_{fsa}) (ms^{-1}) for *Pollachius virens*.



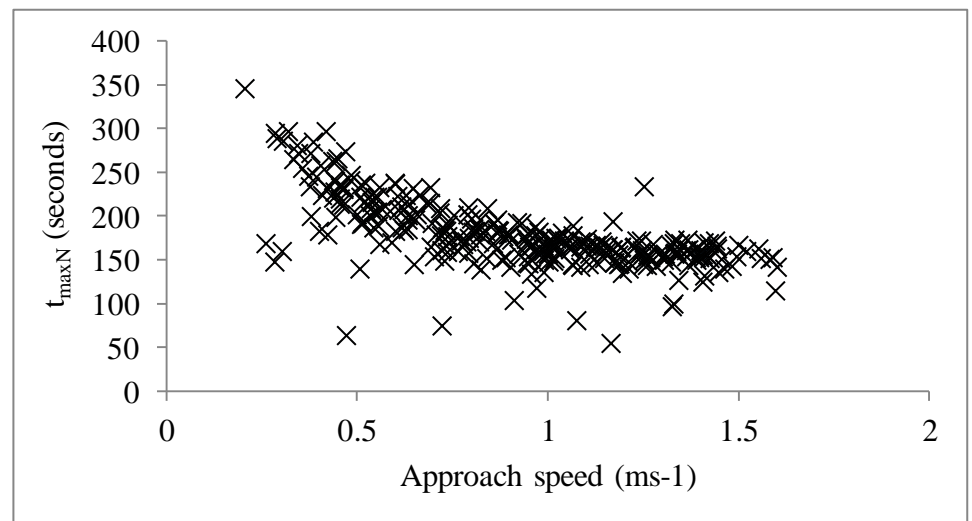
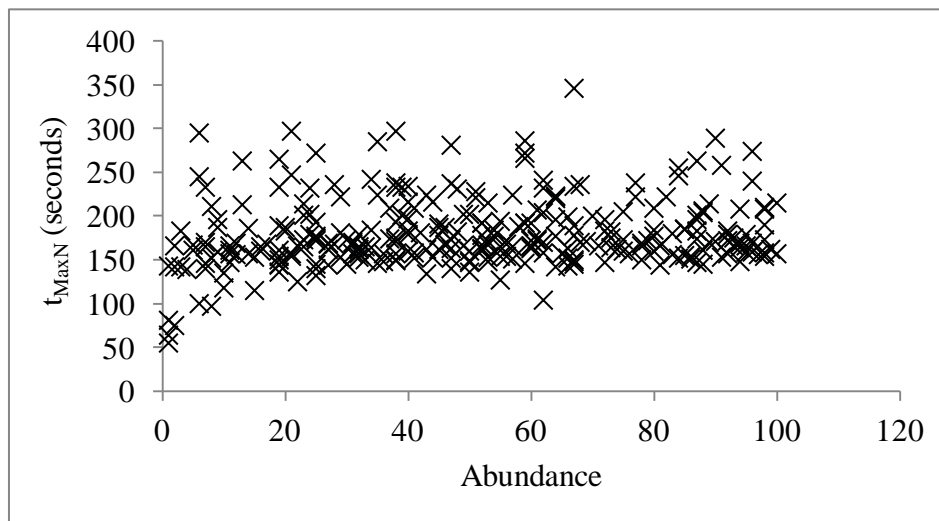
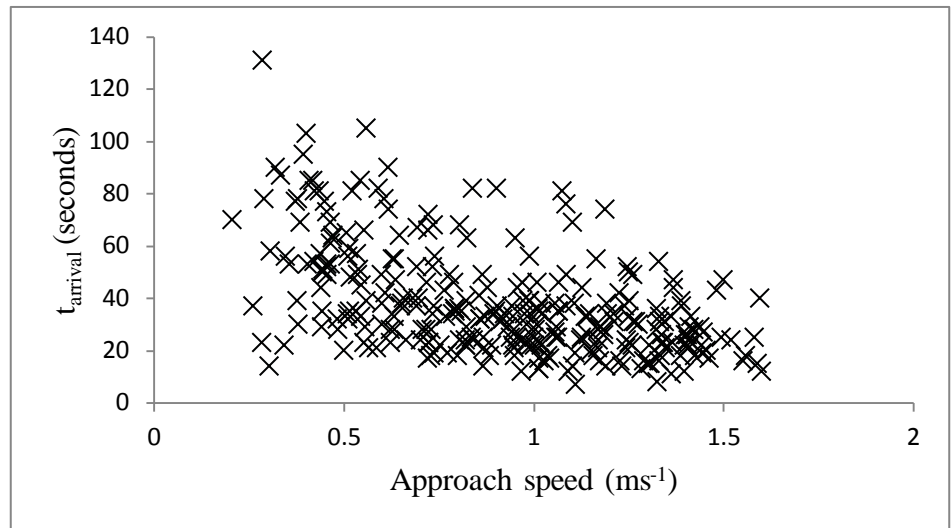
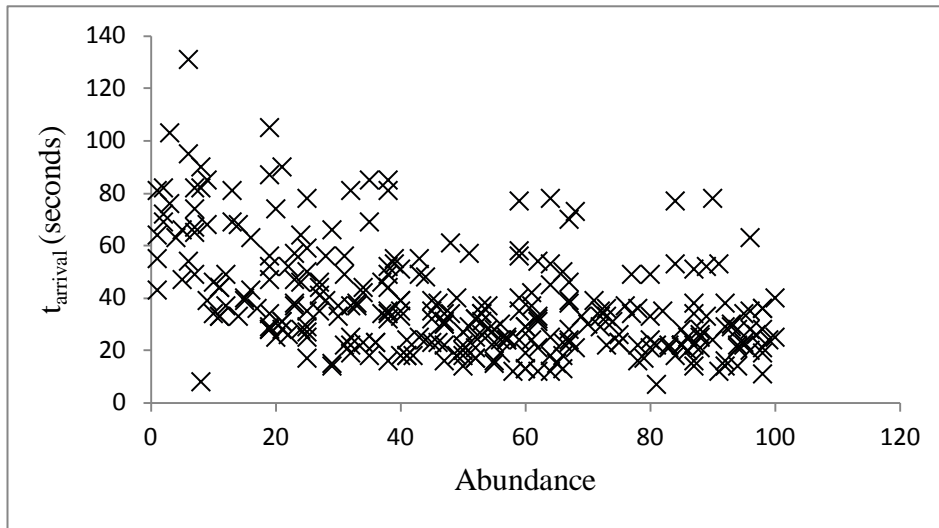
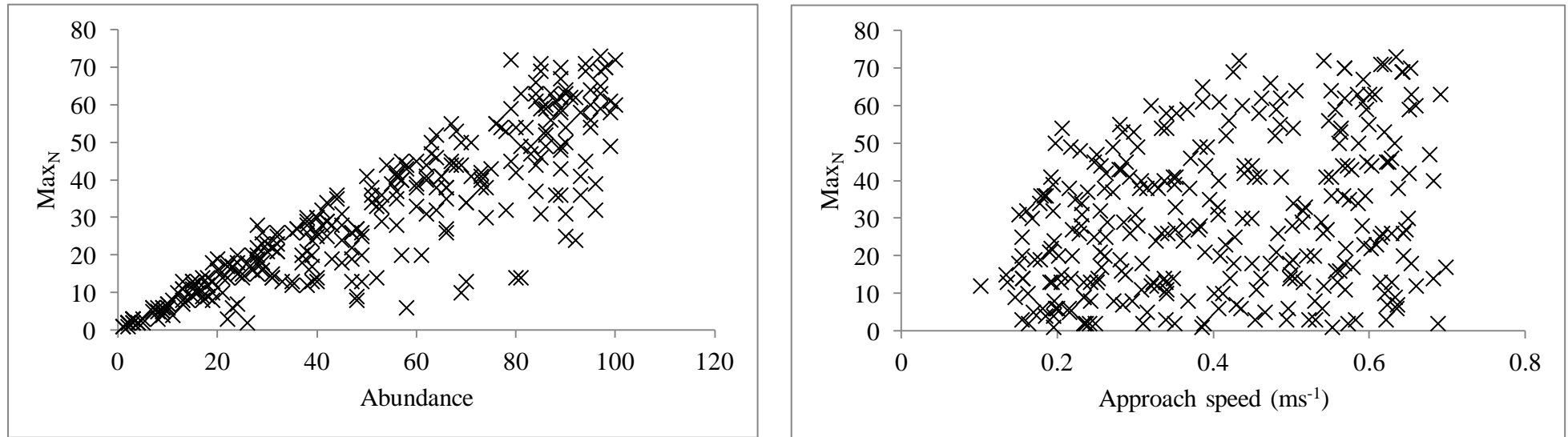
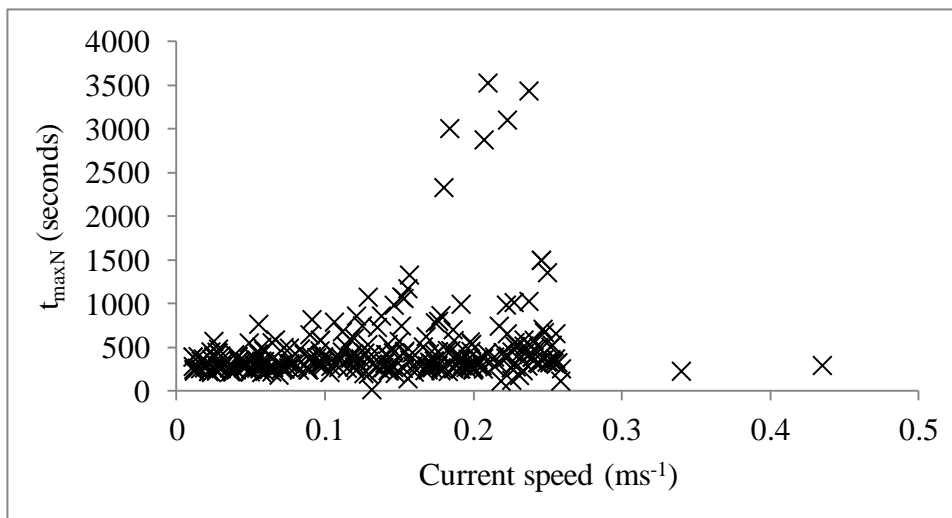
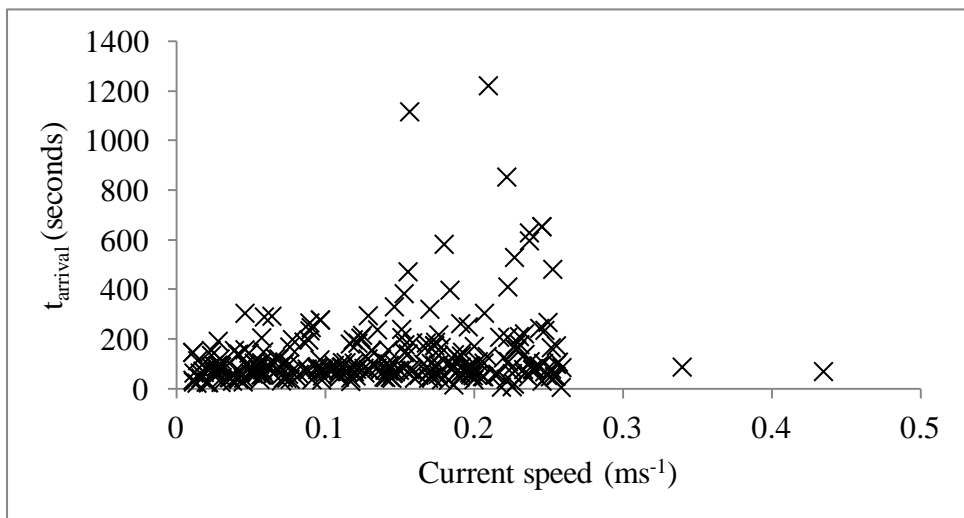
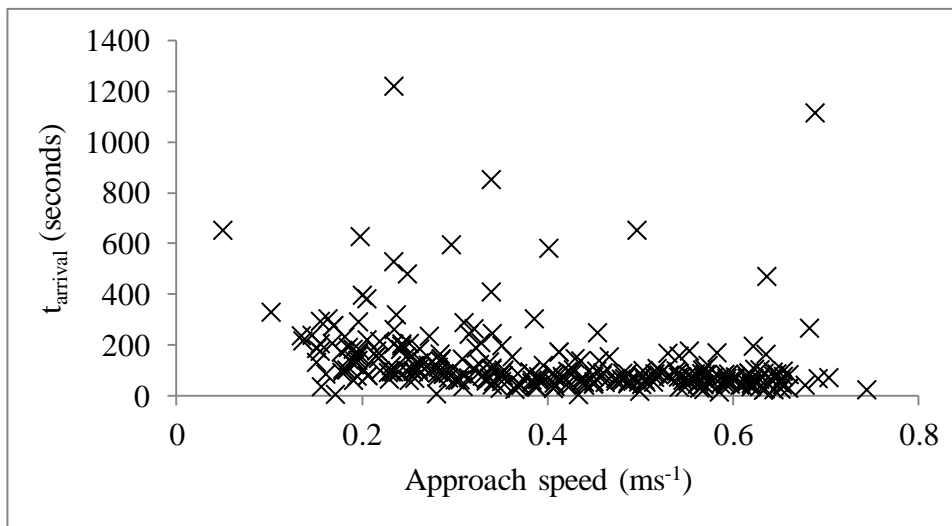
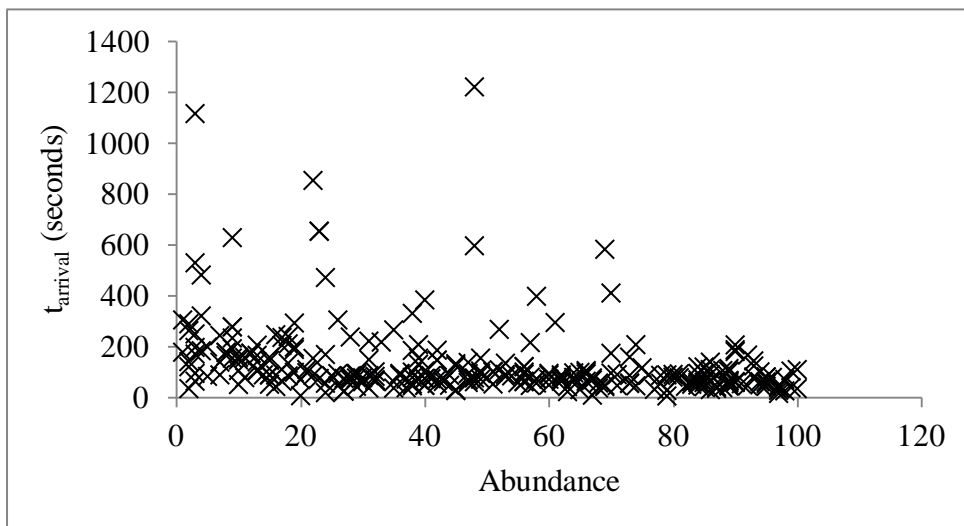


Figure 5.6. Scatter plots of the significant regression relationships between Max_N , t_{arrival} and t_{maxN} and input parameters abundance, current speed (V_w) (ms^{-1}) and approach speed (V_{fsa}) (m s^{-1}) for *Scyliorhinus canicula*.





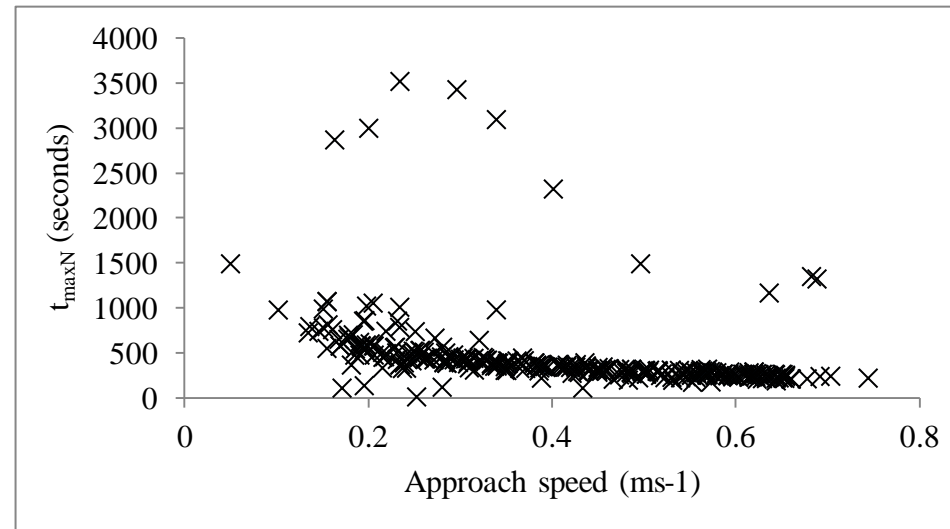


Figure 5.7. Scatter plots of the significant regression relationships between Max_N , t_{arrival} and t_{maxN} and input parameters abundance for *Ephinephelus fasciatus*.

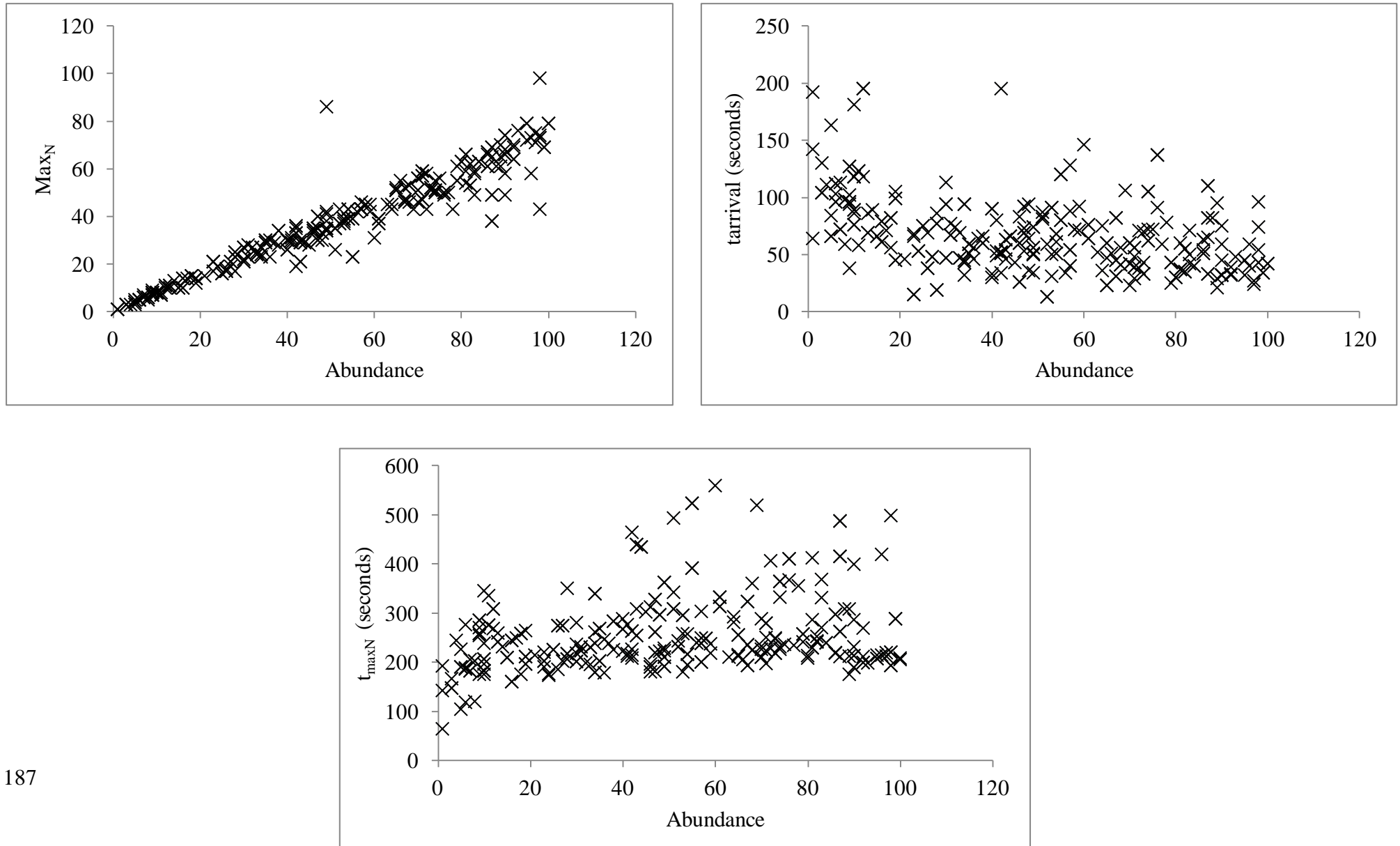
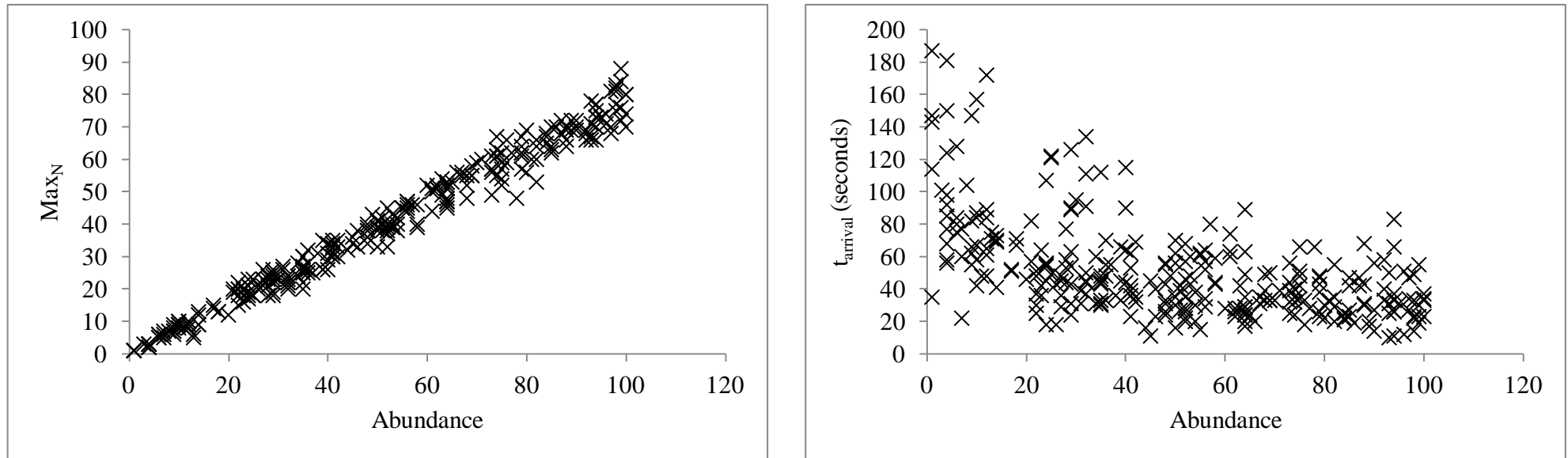


Figure 5.8. Scatter plots of the significant regression relationships between Max_N , t_{arrival} and t_{maxN} and input parameters abundance and current speed (V_w) (ms^{-1}) for *Gymnothorax spp.*



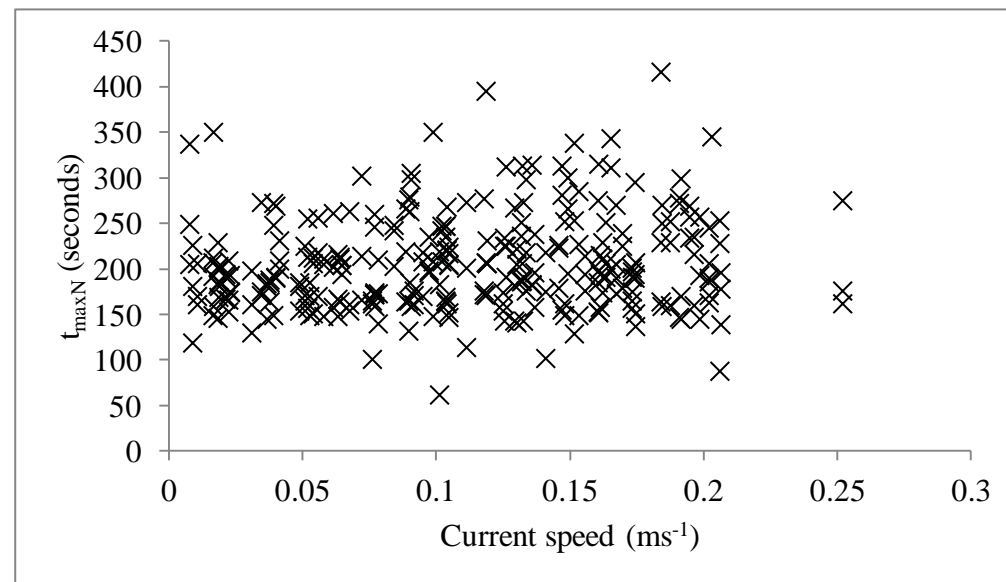
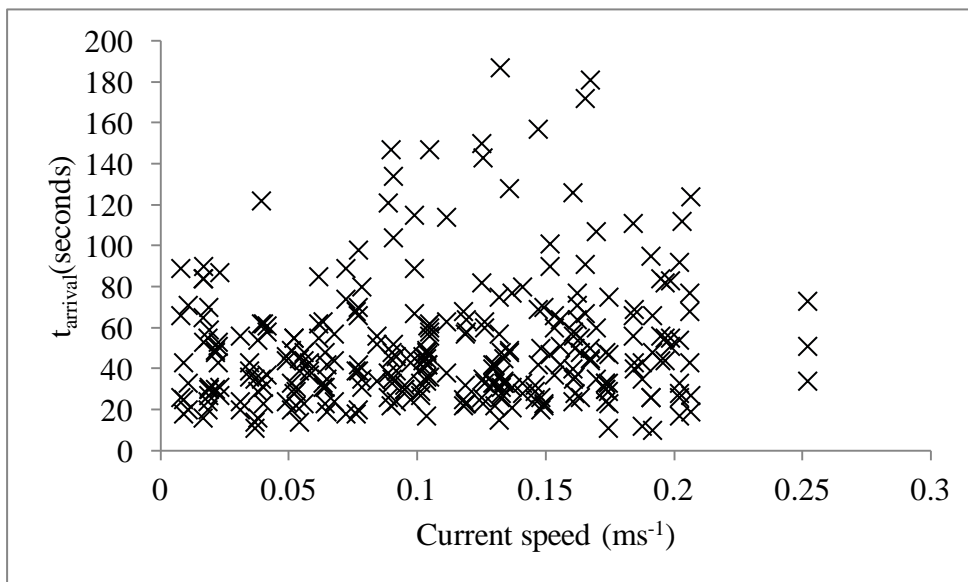


Figure 5.9. Scatter plots of the significant regression relationships between Max_N , t_{arrival} and t_{maxN} and input parameters abundance and *Odontaster validus*.

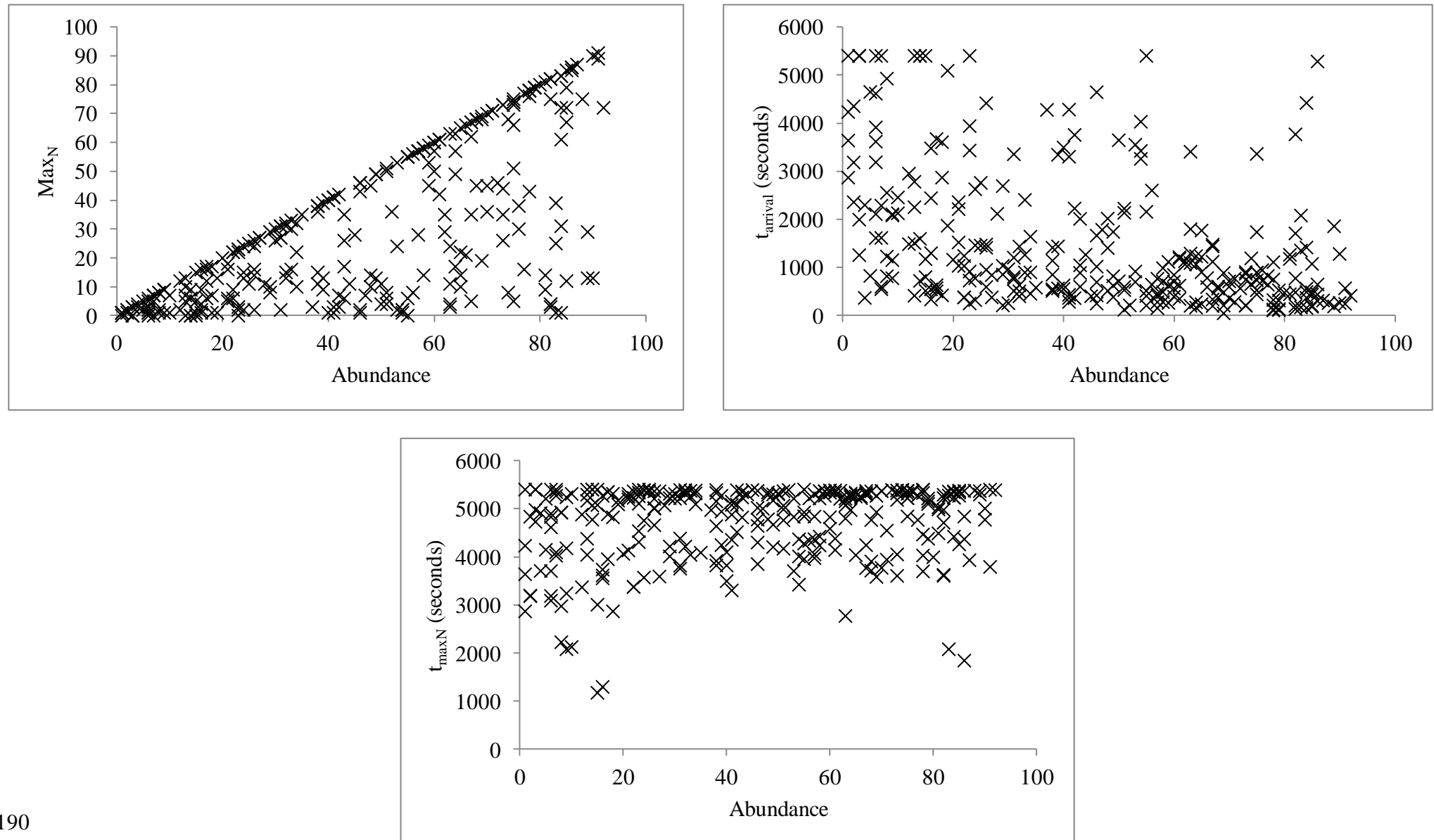
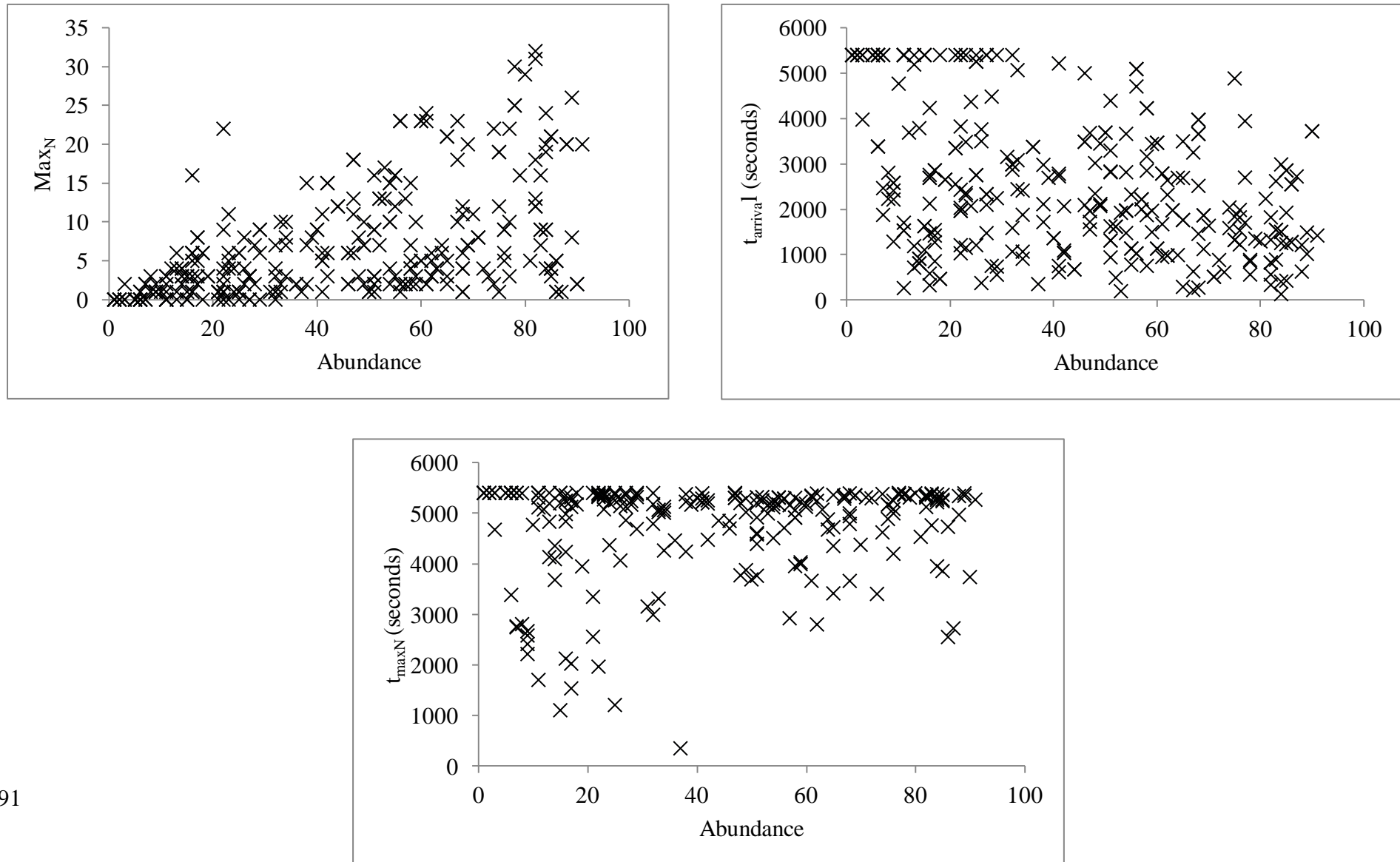


Figure 5.10. Scatter plots of the significant regression relationships between Max_N , t_{arrival} and t_{maxN} and input parameters abundance and *Parbolasia corrugatus*.



5.5.2. Comparison to Baited Underwater Camera data

5.5.2.1. *Tropical Models*

The Max_N output of the two models developed to describe the behaviour of the two tropical fish species; *E. fasciatus* and *Gymnothorax spp*, were both primarily affected by the population abundance input into the models. Therefore, Max_N was used to match arrival patterns from the *in situ* BUC deployment and the multiple model arrival patterns. There was limited evidence from the sensitivity analysis of the effect of the other model parameters on the model abundance indices therefore parameters were kept within the ranges reported in Table 5.1.

For 10 of the BUC deployments the corresponding UVC recorded no groupers and for three of the UVC transects that observed groupers none were observed in corresponding BUC deployments. 10 corresponding UVC and BUC pairs both recorded *E. fasciatus* and for 9 of these pairs the BUC model produced the same or slightly higher abundance estimates (5.11 a). The Bland Altman plot provides little evidence of systematic bias between the abundance estimates of the grouper *E. fasciatus* generated by the BUC model methodology and the UVC surveys. This is concluded as all data points are within the 1.96 SD limits of agreement in the plots and points are distributed symmetrically around the mean (5.12a). A bias, or the average discrepancy, between the abundance estimates measured by the two methods was 0.53 individuals higher in the BUC model.

Only 4 corresponding UVC and BUC pairs both observed moray eels of the genus *Gymnothorax* and the BUC model produced higher or the same abundances. Moray eels were only observed in BUCs in 8 of the corresponding UVC and BUC pairs and only in UVC in 4 pairs (5.11b). The Bland Altman plot s show that points are symmetrically distributed around the mean and that all point were within the 1.96 SD limits of agreement (5.12b). The bias between the abundance estimates from the two methods was recorded 0.4 individuals higher in the BUC model.

5.5.2.2. *Antarctic Models*

The Max_N output of the two models developed to describe the behaviour of the two tropical fish species; *O. validus* and *P. corrugatus*, were both primarily affected by the

population abundance input into the models. Therefore the relationship between Max_N and abundance was used to find a match between the multiple model arrival patterns and that from the *in situ* BUC deployment. From the sensitivity analysis the effect of all other model parameters appeared to be minimal therefore all parameters were kept within the ranges described in Table 5.1.

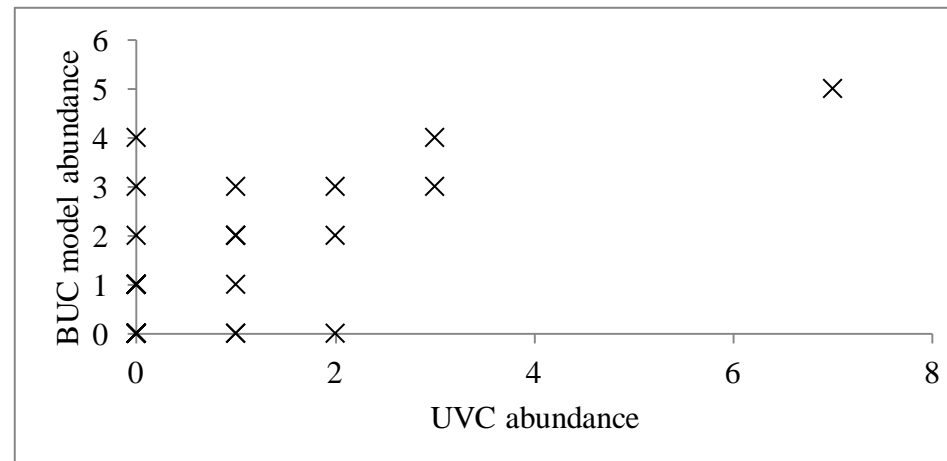
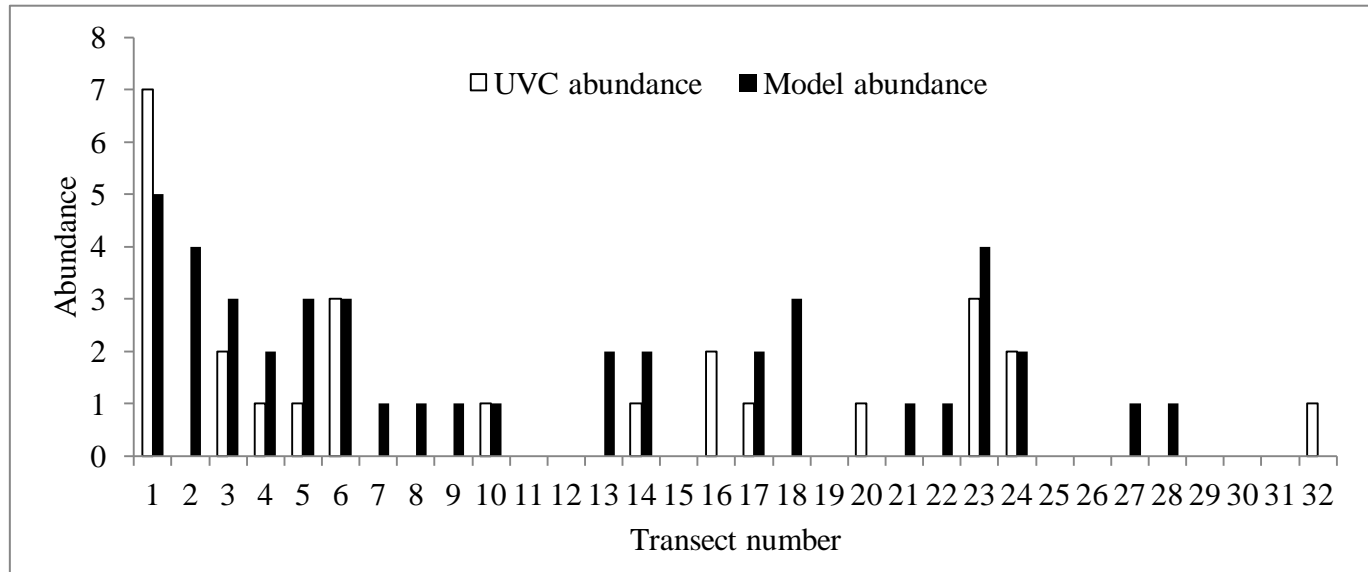
In all 18 UVC and BUC pairs *O. validus* was observed and there was no clear pattern of differences between the abundance estimates recorded by each method (5.11c)

All the data points for *O. validus* abundance estimates from the BUC model and the UVC were within or on the 1.96 SD limits of agreement. From the plot it would however, appear that the plots were slightly asymmetrical to the zero and that average abundances from the model are slightly less than those recorded by the UVC as the abundance of *O. validus* increases (5.12c). The bias in *O. validus* abundance estimates from the two methods was 5.67 individuals more in the UVC surveys.

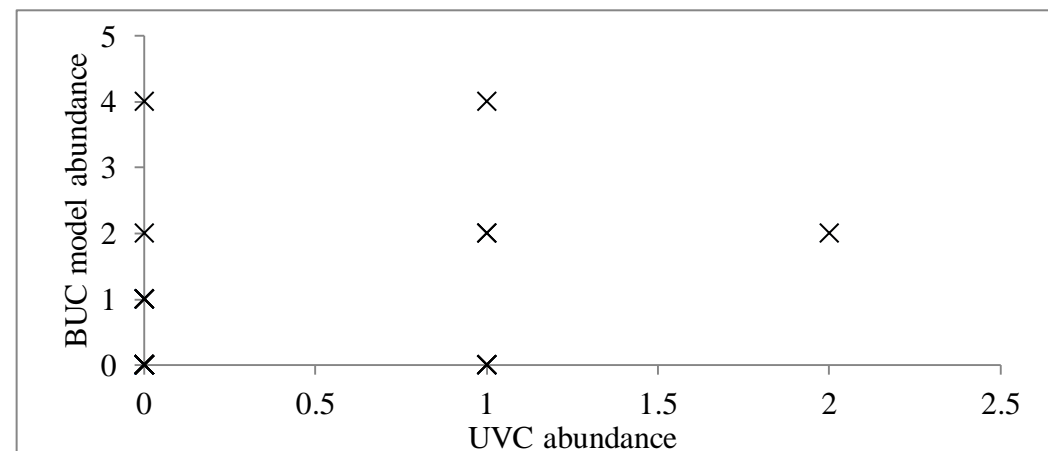
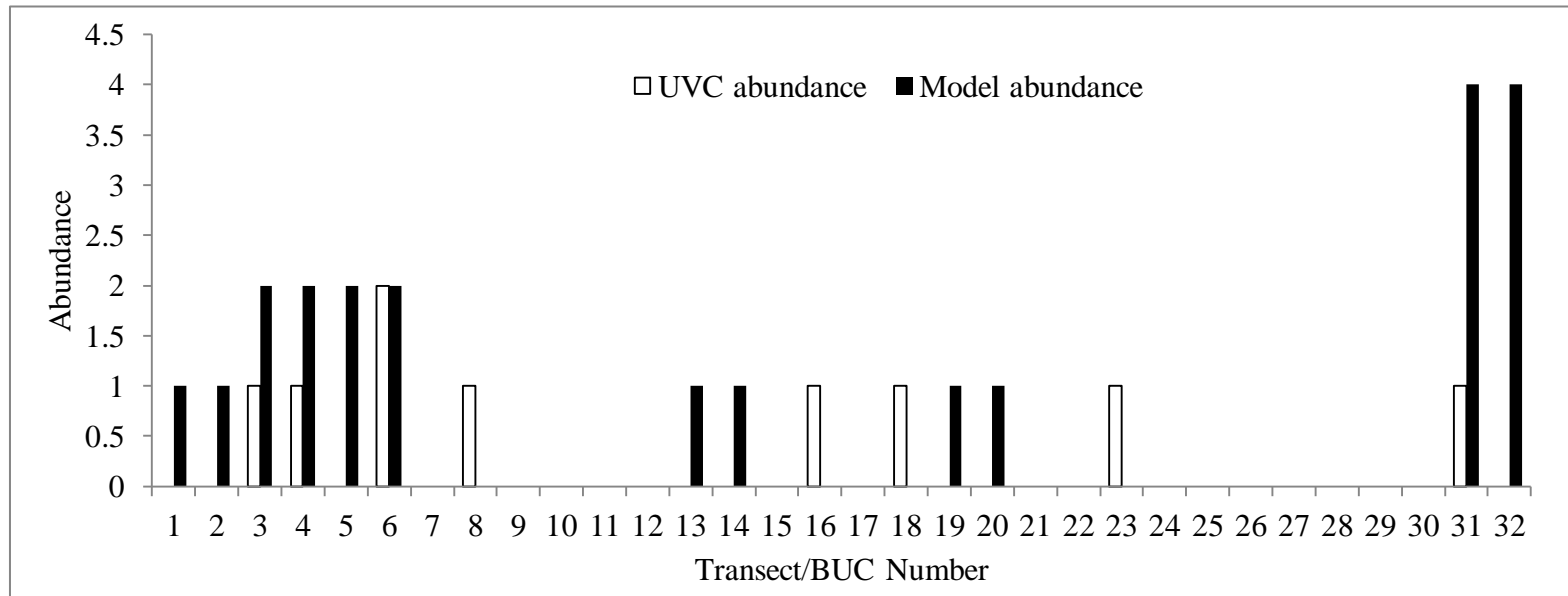
For 8 of the 18 corresponding transect and BUC model pairs abundance estimates for *P. corrugatus* were only recorded by the BUC model and in a further 6 pairs the BUC model estimates were much larger than in the UVC surveys (5.11d). In the Bland Altman plots two outliers were removed where abundances > 100 individuals were recorded by the BUC. All points were within the 1.96 SD limits of agreement but they were not symmetrically distributed around the mean indicating that higher abundances were measured by the BUC. The bias between the *P. corrugatus* abundances recorded by the two methods was 2.93 individuals (5.12d).

Figure 5.11 (a – d). Histograms and scatter plots comparing the absolute abundance estimates generate from UVC transects (open bars) and BUC models (closed bars) for a) the grouper (*E. fasciatus*), b) the moray eel species (*Gymnothorax spp.*), c) the Antarctic asteroid (*O. validus*) and d) the Antarctic nemertean worm (*P. corrugatus*).

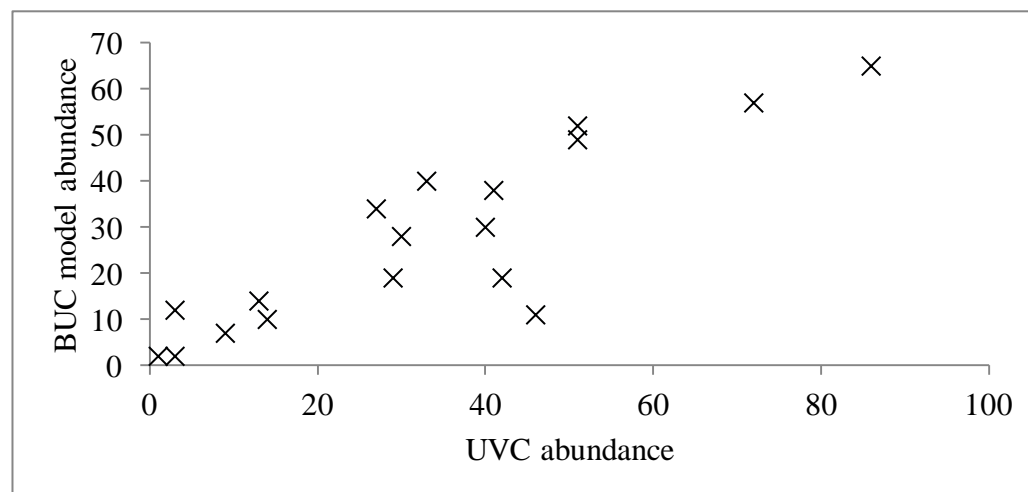
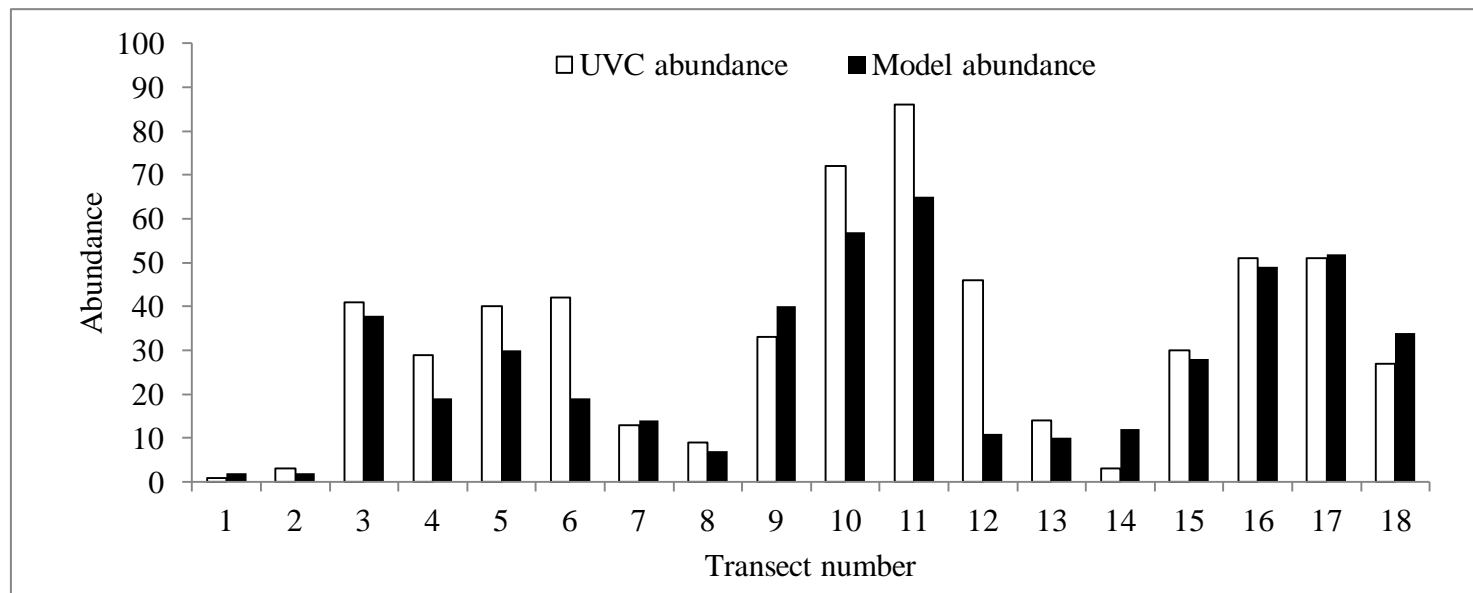
a)



b)



c)



d)

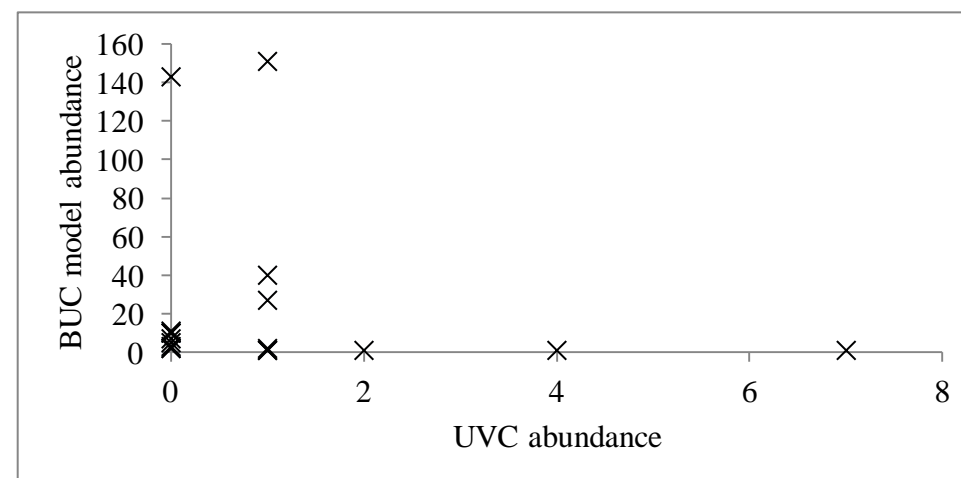
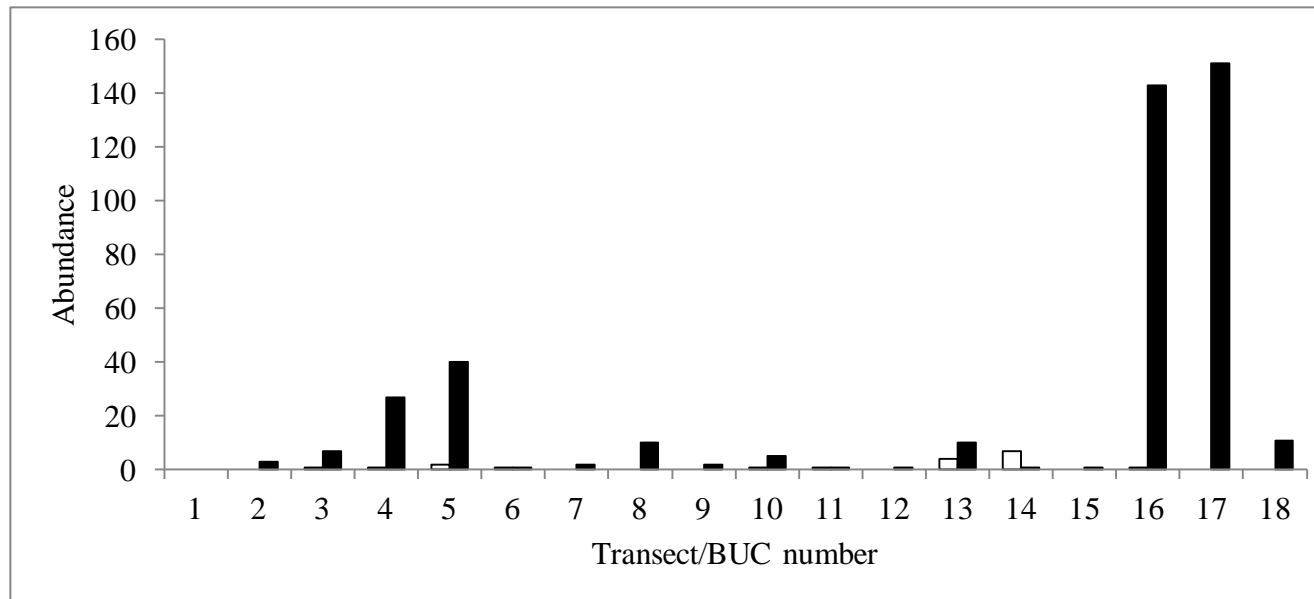
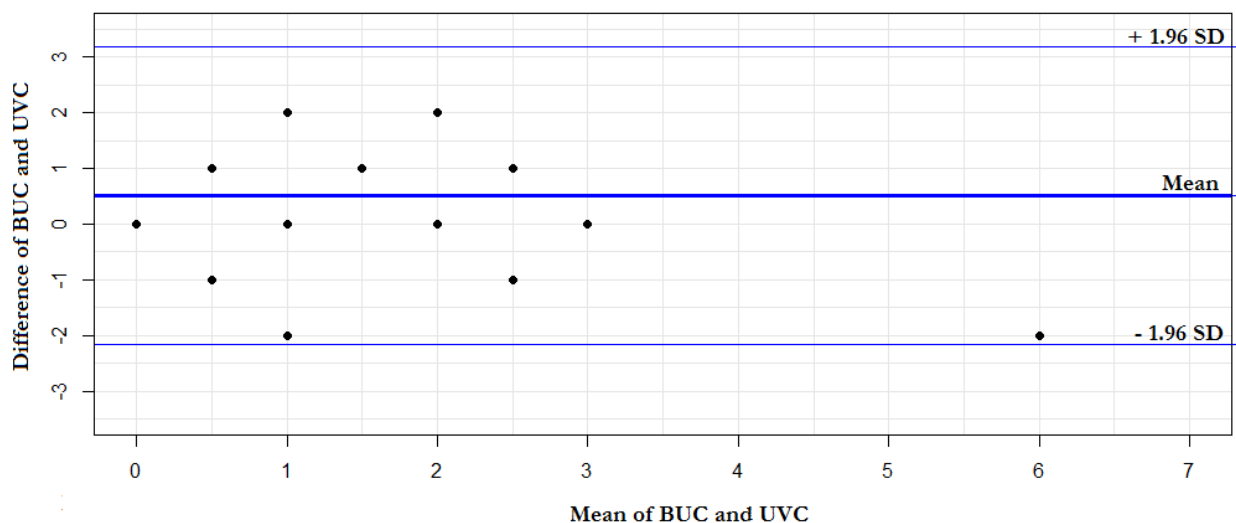
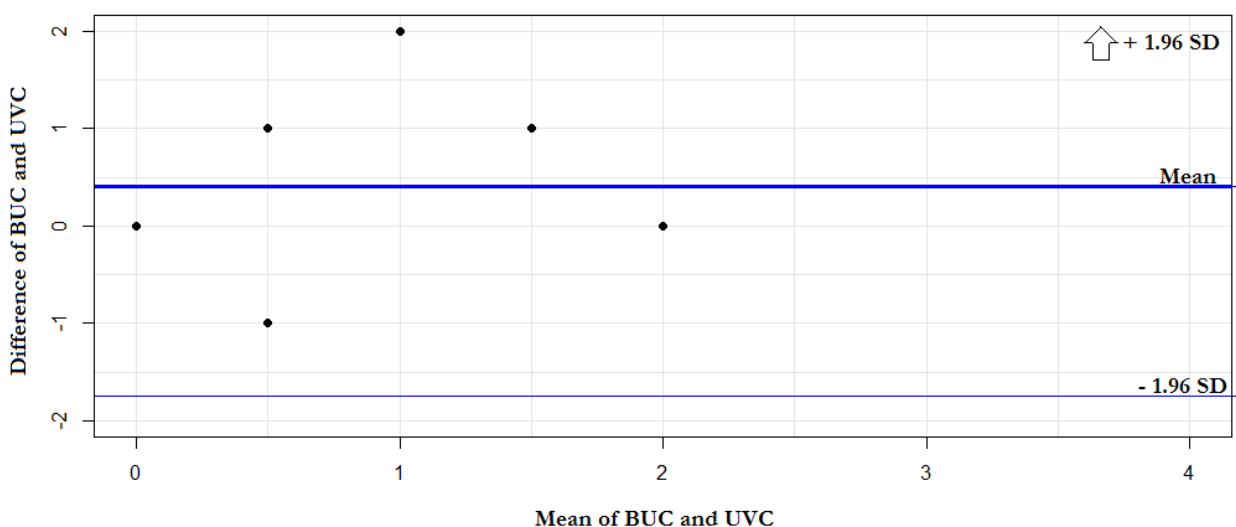


Figure 5.12 (a – d). Bland Altman plots illustrating the agreement between the abundance estimates generated by the baited underwater camera model (BUC) and the underwater visual census survey (UVC) for a) *E. fasciatus*, b) *Gymnothorax spp.*, c) *O. validus* and d) *P. corrugatus*.

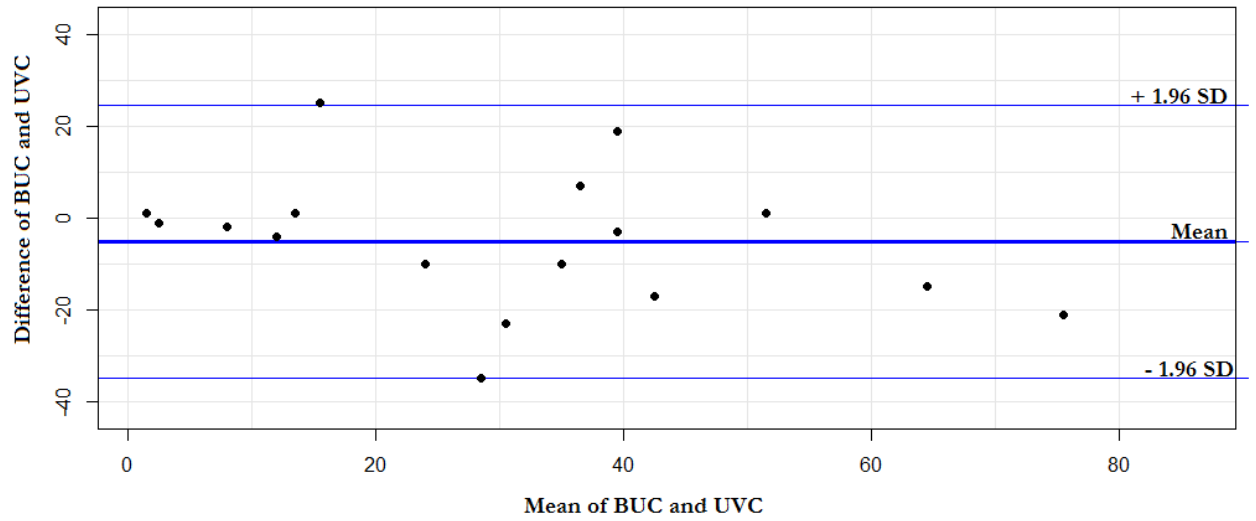
a)



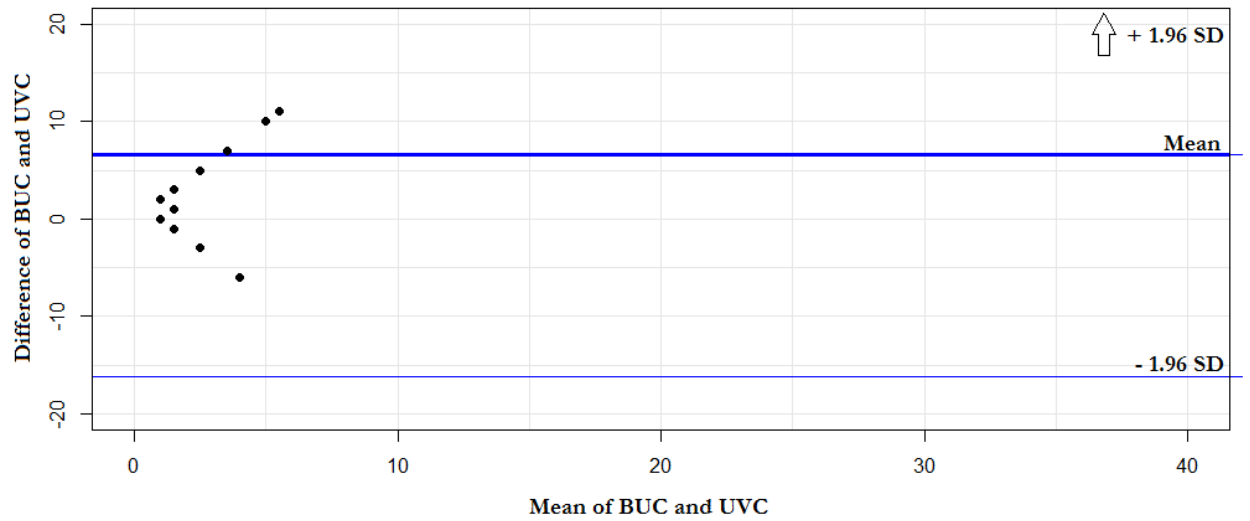
b)



c)



d)



5.6. Discussion

Results indicate that for temperate, tropical and Antarctic models of fish and invertebrate movement around the BUC system the abundance of the surveyed population was the factor causing the largest proportion of the variability of the Max_N generated by the species-specific models. These models effectively allow a BUC user to determine the relationship between Max_N and the abundance of the focal species. The slope of this relationship varies between species but the use of this model system allows the commonly-collected Max_N unit of relative abundance to be converted to absolute units.

Two other commonly-recorded indices of abundance, time to the arrival of the first individual (t_{arrival}) and the time to reach Max_N (t_{maxN}) appear to be less closely related to absolute abundance than might have been assumed. Within the range of species used here, estimates of their searching speed and staying time had relatively little influence on the model Max_N . This is a reassuring finding as it is relatively difficult to estimate these behavioural values in wild animals.

When Max_N was used to find a match between the multiple model arrival patterns and that from the *in-situ* BUC deployments the absolute abundance estimates of *E. fasciatus* and *O. validus* generated by the BUC model methodology were found to be most comparable to the abundance estimates from corresponding UVC surveys. This is because these species are visible to the UVCs as well as to the BUC. The other two species tend to be hidden in rocks or within the coral reef except when bait is present, with their occasional appearance in the open probably being caused by recent feeding or disturbance. The discrepancy between the methods is therefore due to the UVC abundance estimates often falling to zero when in fact the animals are present.

5.6.1. Sensitivity Analysis

For all species-specific, models Max_N appeared to be the measure which accounted for most of the variability in the input population abundance fish or invertebrates.

Measurements of t_{arrival} and t_{maxN} would however, reflect more about aspects of fish approach swimming speed and the current velocity observed around the BUC deployment. Stoner et al (2008) found that a poor correlation exists between BUC time based metrics

and abundance estimates of juvenile Pacific cod from corresponding seine net trawls, while Max_N measures correlated well with trawl survey results. Time based metrics provide less information on the abundance or movement of the surveyed population in relation to the BUC. Time based metrics from BUC studies in the abyssal environment have however, been used successfully to calculate the absolute abundance of scavenging fish populations (Priede and Merrett, 1996).

The current speeds observed around the BUC deployments and that were used for model ranges were relatively slow. If BUC deployments were within environment experiencing high current speeds then possibly variation in current speed would likely have a greater affect on BUC output indices and detailed current speed measurements during BUC deployments would be essential. Diffusional velocity had no significant effect upon the arrival pattern of fish in the Temperate models. However, estimates of the range of diffusional velocities experienced in the tropical and Antarctic environments were not available to investigate it potential effect upon arrival patterns. The incorporation of fluid dynamics modelling into the methodology would enable the potential effects of current speed and diffusional velocity on the arrival of fish or invertebrates at the BUC to be explored in more detail.

Staying time had no impact on abundance metrics even though it had been shown to affect Max_N values in the deep sea BUC studies (Priede et al. 1991). The staying time used was an approximate measure and for the fish these were much shorter than has been observed for deep sea BUCs. The Antarctic invertebrates did not leave the bait within the timescale of the BUC deployment. The majority of BUC studies in the abyssal northeast Atlantic found that the mean staying time of the deep sea grenadier (*C. armatus*) to be approximately 2 hours (Priede et al. 1994, Henriques et al. 2002). However, Jones et al (1998) estimated the mean staying time for scavengers to be 27 minutes and observed a maximum for 2 hours 50 minutes. In the shallow water BUC fish arrive more rapidly and frequently, causing the staying time to likely have less of an impact on Max_N values. With longer staying times the number of fish at the camera will accumulate to reach Max_N meaning that Max_N will have more of a linear relationship with the numbers visiting the BUC. However, in the shallow water environment where more fish are coming and going from the field of view there is more uncertainty whether Max_N will reflect the actual numbers that visited the camera.

These results therefore indicate that in these models accurate estimate of fish or invertebrate staying time, cruising speed or diffusional velocity are not important to the output of the model and therefore the selection of a suitable range is appropriate. It would be more recommended that more efforts are put into gathering accurate estimates of fish and invertebrate approach speed and the current speed, primarily within the Temperate environment.

5.6.2. Model and UVC Abundance Estimate Comparison

The abundance estimates generated by the BUC modelling methodology and the UVC were found to be comparable for both tropical fish. However, in a number of BUC and UVC corresponding pairs the BUC survey observed moray eels when the UVC surveys recorded none causing the BUC model to estimate abundances when the UVC estimate equalled zero. Moray eels of the genus *Gymnothorax spp.* are generally nocturnal hunters and during the day they will remain hidden within rocky refugias (Bshary et al. 2006, Bardach et al. 1959) making it difficult for daytime UVC surveys to detect them. The biases between the abundances of *E. fasciatus* and *Gymnothorax spp.* recorded by the BUC model and the UVC are relatively low but should be considered in terms of the accuracy and precision required by a monitoring programme.

The abundance estimates generated by the BUC models for the Antarctic asteroid *O. validus* were comparable to those generated by the corresponding UVC surveys. However, the abundance estimates generated by the BUC models for the nemertean worm *P. corrugatus* were higher than those within the higher abundance estimates were produced by the BUC models for *P. corrugatus* due to the BUC recording *P. corrugatus* but none being observed in the corresponding UVC survey. This can be attributed to the species taking refuge under rocks during the day (Clarke et al. 1997) resulting in very few being observed in daytime transects thus incorrectly reducing the populations densities to which the models was parameterised calibrated to being artificially low. Little is known about the behaviour of *P. corrugatus* and it is possible that large groups of individuals congregate within refugia, violating the assumption of the model that individuals are randomly distributed and act independently of each other. *O. validus* would appear to be easily observed in transect during the day and was commonly observed in both BUC and UVC surveys.

5.6.3. Model Improvements

Models also assume that all fish react and follow the bait plume once encountered, however factors such as satiation state, olfactory capabilities and the availability of other food sources in the environment will impact upon their decision. Due to the comparability of absolute abundance estimates from the BUC model and the UVC, it would appear that a large proportion of these species react to the bait plume. Model assumptions include that individuals react independently of each other however, competitive behavioural interactions have been observed to occur between fish at the bait of BUC systems (Armstrong et al. 1992, Stoner et al. 2008). It has been suggested that these interactions discourage some fish from approaching the bait due to the increased chance of competition (Jones et al. 2003, Willis et al. 2003, Cappo et al. 2004) or predation (Lampitt et al. 1983, Harvey et al. 2007) presented by the other fish. It is therefore evident that in both the fish and invertebrate species studied competitive interactions around the BUC could potentially impact upon the arrival patterns of individuals at the bait. The effect of other species interactions on the arrival patterns of fish and invertebrates at the BUC should also be considered. Effects may include particular species posing a higher predation risk at the bait reducing the number of the other species observed. Further studies of the impact of these interactions would allow this information to be added to modelling approaches. The modelling methodology however, provides a framework within which multiple species models could be combined using information on the species composition and potentially the effects of interactions on bait approach and staying times. Also when foraging individuals become close to the bait they are potentially attracted by the movement and sounds of others feeding (Bailey and Priede, 2002). For shallow water fish species that rely heavily upon sight for foraging and hunting (Stoner et al. 2007). This has the potential to impact on their behaviour in relation to the BUC system and thus arrival patterns.

Even though staying time had a limited impact on the abundance metrics from shallow water BUC survey the information gathered on this parameter was restricted due to the difficulty in identifying individuals. Information on this parameter could be collected via a mark-recapture based studies either using external tagging or pattern recognition software. Stereo video systems could identify individuals based upon size measurements to

provide measurements of staying time. Further valuable research would be the investigation of the application of this modelling approach to other marine species which have been found to be attracted to BUC systems. This would primarily include the large, predatory mobile species that BUC surveys have been found to effectively survey (Malcolm et al. 2007, Watson et al. 2010). The ability of temperate models to generate abundance metrics comparable to those of in-situ BUC surveys also remains to be assessed.

5.6.4. Application of Methodology

Preliminary results show that this stochastic modelling approach can generate absolute abundance estimates of some shallow water fish and invertebrate populations from BUC deployments and that these estimates are comparable to an established survey method. The generation of absolute abundance estimates from shallow BUC surveys improves the application of the method substantially and makes the results comparable to those of other survey methods, such as trawl surveys and transects commonly used in stock assessments and monitoring programmes. This also enables previously-collected BUC data to be reanalysed and diversity indices for these deployments to be recalculated based on the abundances of the animals present rather than combinations of Max_N values..

5.7. Conclusion

In conclusion, the spatial, stochastic modelling approach described and tested in this study represents one of the first attempts to model the arrival process of shallow water marine species at a BUC system. Initial results for a small set of temperate, tropical and Antarctic species-specific models show that this method has the potential to generate absolute abundance estimates from BUC data that are comparable to UVC data. This development combined with the existing ability of BUCs to generate data in a time-and-cost efficient and non-destructive manner can significantly improve the value of this method to monitor inshore marine populations.

6. Final Discussion

6.1. Marine Conservation and Management

Gathering information on the biodiversity and abundance of marine species is important to achieve effective marine management. Destructive sampling methods such as trawling, are becoming more unsuitable as many marine populations decline and with the increasing development of MPA networks. Remote and non-destructive sampling methods, such as underwater camera survey systems, are therefore becoming increasingly important to the monitoring of marine biodiversity. BUCs in particular have been identified as an effective methodology to provide information on the relative abundance of fish and invertebrate species of commercial and recreational importance. Advancements in this area will therefore be particularly beneficial to the management of these species.

6.2. Advancements in the Field of Baited Underwater Camera Surveys

The majority of BUC surveys have been conducted in areas where the visibility is relatively clear, either in tropical Western Australia (Watson et al. 2010, Harvey et al. 2012) or temperate New Zealand (Willis et al. 2003). This thesis describes the development of a BUC system capable of providing clear images and data on the arrival patterns of inshore fish and invertebrate assemblages in temperate and Antarctic inshore water where visibility can be poor. In particular, a cost-and-time efficient system suitable for conducting surveys in the difficult conditions of the temperate waters of the West coast of Scotland. The study described in Chapter 2 represents the first BUC surveys in Scotland's only no-take zone and has demonstrated how the system can provide information on the potential associated changes in fish and invertebrate assemblages. The method has the potential to play an important role in monitoring the impact of Scotland's future network of MPAs on inshore marine communities and the study in Chapter 2 provides baseline data in the Firth of Clyde against which future BUC studies can be compared. A wide variety of temperate species are attracted to the camera system, many of which are of commercial and recreational interest demonstrating the ability of the method to provide information on these species to help in their management.

The Gulf of Aqaba is a distinct biogeographical region of the Red Sea that supports unique reef fish assemblages and the study described in Chapter 3 represents the first use of a BUC system in the area. It is important to conduct a separate study to understand the application of the BUC method in this area due to the unique nature of the fish assemblages and to determine whether BUC could be used as an additional survey method to the current UVC survey method. The BUC was able to provide information on the species richness of predatory fish species, which are important to understand the impact of the local MPA, using a lower effort to the UVC surveys. However, the UVC appears to be the most appropriate means of assessing change in fish abundance at least until improved BUC metrics are developed. The results in Chapter 3 highlight that the assumption of many BUC based studies that abundance estimates are comparable to UVC estimates needs to be tested.

The use of BUC systems has primarily been applied to determine the effect of MPA establishment on inshore fish assemblages (McLean et al. 2010, Willis and Babcock, 2000) and some studies have focused on habitat associations (Moore et al. 2010 and Bond et al. 2012). The work presented in Chapter 4 demonstrated the potential application of the BUC system to examine further other biological questions and examine patterns in Antarctic shallow water marine communities in relation to iceberg scouring. This built on previous BUC work in the area and represents the first examination of how scavengers are affected by the recognised pattern of decreasing iceberg scouring frequency with depth. Results indicate that different scavenger species are adapted to high and low iceberg scouring environments and that they are distributed in accordance with the recognised pattern of decreasing iceberg scouring frequency with depth. This provides a significant advancement in the knowledge of the dynamics of shallow water marine communities in this highly disturbed environment.

To date, the data from shallow water BUC surveys has been primarily used for comparisons of relative abundance (Willis and Babcock 2000, Stoner et al. 2008). The development of a modelling approach for the first time for shallow water BUC studies has shown potential to enable absolute abundance estimates to be generated from BUC arrival patterns. From the preliminary work it appears that the modelling approach has the potential to significantly advance the application of the method in the monitoring of mobile predatory and scavenging species. This information is particularly important as these

species are often of commercial and recreational interest and can act as indicators of the health of the marine environment. Abundance estimates of these species will also be important when determining the impact of the creation of MPAs. This methodology also provides a means by which to monitor these species with the minimal use of destructive trawl surveys. This will both limit the number of UVC diver or trawl surveys required to gather information on the density of these species and overcome some of the issues associated with monitoring using UVCs, as discussed in detail in Chapter 1 and 3. UVC or trawl surveys will only be necessary to gather data to test model outputs during development. The potential use of BUCs to gather abundance data on marine populations, limits the reliance on diver surveys which is particularly useful in Antarctic and temperate waters where diving is especially cost and time heavy and highly dependent on good field work conditions. This was demonstrated during field work in Antarctica when the BUC system could be deployed in poorer weather conditions and at deeper depths than divers could operate.

6.3. Recommendations for BUC surveys

From the results of this thesis it is recommended that when future BUC studies are introduced to new areas the comparability of the BUC abundance indices to those from more established methods, such as UVC surveys, is measured. It would also be recommended that established BUC studies compare BUC abundance metrics with abundance estimates from other methods to test whether assumptions that the measure are comparable are correct. For BUC studies to advance from producing measures of relative abundance to produce measure of absolute abundance will involve an estimation of the effective bait plume area and a means to account for the movement and behaviour of fish in relation to the bait plume and the BUC. The modelling approach described in this thesis provides a framework within which these processes can be modelled and has been demonstrated to have the potential to produce absolute abundance estimates that are comparable to estimates from UVC surveys for some species. It would therefore be recommended that in future BUC surveys a current meter should be deployed along with the BUC to ensure that current speed information is collected to be used in modelling methodologies. For the models described in this thesis fish swimming speed prior to detection of the bait and staying time appeared to have a limited impact on arrival patterns at the bait. However further collection of fish approach speed would potentially improve

their application. Max_N represents one of the most commonly collected metrics from BUC studies and a large volume of data already exists for shallow water BUC studies. This data could potentially be converted to abundance estimates if current meter data is also available. Field measures of fish or invertebrate approach speed, cruising speed and staying time should also be made. Future work could begin to consider the impact of other factors, such as competition and satiation state, on fish and invertebrate arrival patterns. The model framework currently only deals with individual species but in reality a BUC system attracts a range of scavenger and predatory species. It would therefore be important to consider how the modelling methodology can be used to model the movement and arrival of multi-species assemblages at the BUC. This would involve a detailed knowledge of the interactions between species arriving at the BUC, but much of the data required to understand this will be available in existing video recordings. It is one of the great strengths of the BUC method that the original images or video can be reanalysed in new ways as methods improve, whereas for UVCs the only data source will be whatever the diver thought important at the time of the dive or had been told to record.

6.4. *Future Studies*

Future studies should focus on the furthering of modelling approaches and the development of species-specific models taking advantage of the large body of shallow water BUC data currently available. Many previous BUC studies have been conducted alongside UVC estimates of abundance (Watson et al. 2010, Langlois et al. 2006) and would provide data to compare model outputs. Calculation of fish approach speed around the camera using the recent developments in stereo camera techniques is highly recommended. Currents dynamics are complicated in the shallow water environment and further refinements in the modelling of the bait plume dynamics in this approach will enable the accuracy to be improved. Plans are already being developed to combine the models of fish and invertebrate movement around the BUC system described in this thesis with a fluid dynamics model used to plot the bait plume area from a BUC. This future work is in collaboration with Dr Alan Jamieson at Oceanlab, Aberdeen, and would enable the bait plume area, shape and odour density to be estimated using field data on the current velocity collected during BUC deployments and inserted into the model to replace the simplified plume shape used here.

6.5. *Conclusion*

Our international commitments to the creation of Marine Protected Areas and for the wider protection of our marine resources will require us to survey and monitor a wider range of marine species and at a higher temporal and spatial resolution than has previously been the case. With all public expenditure being constrained, the need for cost-effective and reliable means of determining the composition of marine communities has never been greater.

Here I demonstrate the development and deployment of a time and cost-effective BUC system capable of surveying marine scavengers and predators in across a wide range of habitat types. I showed that existing BUC metrics could not yet replace UVCs as a survey method, but that BUCs were extremely effective at determining which predatory species were present in an area. Using these simple metrics I was able to demonstrate the effects of iceberg scouring on scavenger assemblages, assessing for the first time the interactions between depth and iceberg exposure.

In order for BUCs to achieve their full potential a means of converting simple BUC metrics such as MAX_N into true abundances is required. In the final data chapter I present a model capable of doing this and a framework into which hydrodynamic models of odour plumes can be inserted. This approach will greatly improve BUC surveys, allowing this method to make its contribution to achieving the daunting tasks which face us.

In conclusion this research has enabled the development of a cost-and time-efficient BUC system that can be used in tropical, temperate and Antarctic environments to answer biological questions regarding the abundance and biodiversity particularly of predatory or scavenging fish and invertebrate species. Initial studies comparing the method to UVCs showed that the standard metrics were not adequate with the focal species. By modelling the behaviour of fish and invertebrates around a shallow BUC a new approach has been developed which should allow true abundances to be estimated in the future. This modelling method can also be applied to existing data sets, greatly adding to their value.

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